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THE INHERITANCE OF POLYMORPHISM AND SEX IN COLIAS PHILODICE[1]

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THERE is perhaps no phenomenon of greater general interest to students of organic evolution than polymorphism, yet, although it is of frequent occurrence in insects, in few cases has it been investigated with long-continued and thorough experiments in breeding. Entomologists have usually been content to prove that different forms arise from the eggs of a single female, or of similar females of the same species, without reference to the male parent or to the immediate ancestors of the female. The time has come when these interesting phenomena, lying at the very doors of those at least who live in the country, demand more serious attention than they have yet received.

Colias philodice, the common yellow butterfly of the clover, called sometimes the clouded sulphur or roadside butterfly, is distinctly dimorphic in the female sex, in that the ground color of the wings is either yellow or white, the yellow female in most localities being much the more abundant. As this common species can readily be bred in large numbers, it affords excellent material for studying the inheritance of dimorphism limited to one sex.

[1] Read before the American Society of Naturalists, December 30, 1910.

Moreover the color pattern, which is the same in both the typical yellow and the albinic variety of the female, differs in the two sexes to such an extent that they may be distinguished even in flight. The wings of the

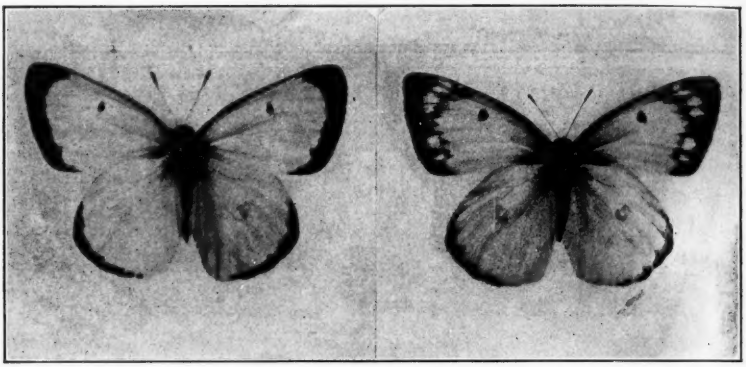

FIG. 1. *Colias philodice*. Male. FIG. 2. Yellow female.

male (Fig. 1) are marked with a solid black band of nearly uniform width extending along their outer margins, whereas in the female (Fig. 2) the marginal band is wider on the fore wings and usually invaded by spots

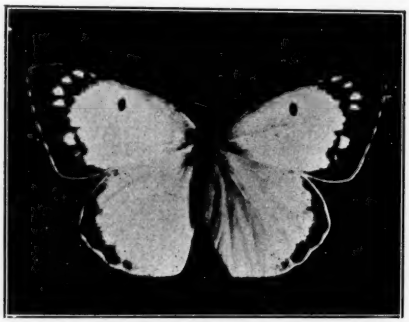

FIG. 3. White female.

of the ground color, but narrower on the hind wings and dusted with scales of yellow or, in the albinic variety, of white. The marginal band on the hind wings of the female in some individuals is absent altogether, the width of the bands in general in both sexes being very variable.

Besides these pronounced secondary sexual differences

in color and the common occurrence of the albinic female, a few specimens have been taken of an extremely rare mutation, the melanic male, in which the yellow is replaced by smoky black, the margin being distinctly paler than the ground color. In geographical distribution this aberration does not seem to follow the general rule laid down by Scudder that melanic forms occur in the southern part of the range of a species, for two of the specimens were from near Montreal, three seen and one captured at Palmyra, N. Y., and one now in the collection of Mr. H. P. Richardson, of Concord, Mass., was taken at Plainfield, Mass.

Partial melanism, or a melanistic tendency, often occurs in the female, though complete melanism has been found so far only in the male. This tendency reappears in successive generations independently of the environment, in certain strains that I have bred, though I think it possible that the action of the surroundings on certain individuals in a plastic condition may turn the germ cells in this direction. I have not yet had an opportunity to test this supposition, and my observations have been almost entirely directed to the inheritance of the albinic variety of the female.

Albinism in the genus *Colias* is due to the replacement of yellow pigment with another which is white (Fig. 3), all other pigments (black, red, etc.) remaining the same. The white is sometimes tinged with yellow, but there is a sharp difference between the color of a typical yellow female and that of the albinic form.

Albinism is not entirely confined to the females, though among the 900 descendants of white females that I have raised there has been not one white male. White males may be expected in regions where the white female is especially abundant. At Hanover, N. H., the proportion of white females to yellow is, perhaps, roughly five per cent. At Ithaca, N. Y., Professor Macgillivray informs me, the proportion of white females is considerably larger, being perhaps 10 or 15 per cent., and at Milton, Mass., Mr. W. L. W. Field estimates them at 20–25 per cent. In two localities where the white male has been

taken, about 50 per cent. of the females are white. These regions are Lava, Sullivan Co., N. Y., reported by Mr. Geo. Franck, and Alstead, N. H., on the authority of Mr. W. L. W. Field, who has seen only one white male, however, during several seasons of field work in that region.

Scudder makes the statement that "In the north this rarely, almost never, occurs in the first brood of the season, and is found much more abundantly in the latest than in the middle brood, the numbers increasing as the season advances." If this statement is true, it has an important bearing on the inheritance of the white character,[2] for he means, of course, that the proportions of the white females to yellow in the spring broods is less than in the later broods. My observations at Hanover in 1909, and those of my collaborator Mr. P. W. Whiting in Cambridge, Mass., in 1910, do not bear this out, for we found the white females in both places quite as common in the spring brood as in those of summer or autumn. Edwards likewise states that in the south the white form is not infrequent in the spring brood. The probable reason for Scudder's observation is that the population of the spring brood in the long run may be relatively small, because many of the hibernating caterpillars perish. The chances of finding white females in the field in the spring after a severe winter may therefore be less than during the flight of the more abundant summer broods that have not been affected by disastrous winter weather.

One of the most interesting observations that I have made during the past two seasons was the discovery of a wild female *Colias philodice* of the spring brood closely resembling *Colias nastes* of Labrador (Fig. 4), with a greenish-yellow field overspread with brownish scales, giving a grayish effect. In the margin brown replaces black. This form of female is not common, and I have seen it nowhere described. It was captured at Hanover, N. H., on June 10, 1909, and produced a brood of 34 butterflies (Fig. 5) of which 19 are males, all of which are yellow, 10 are yellow females, 5 are white females. The yellow and white colors of these offspring are of an

[2] See foot-note, pp. 266, 267.

unusually clear hue, and quite unlike the color of the mother.

The progeny of this female show that, supposing her to have mated with a pure yellow male not carrying white, as was probably the case, she is a heterozygote for

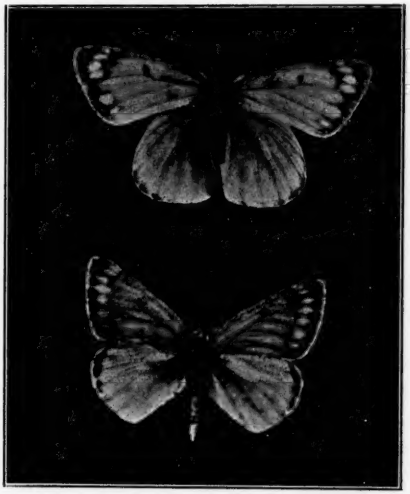

FIG. 4. The upper figure represents a spring form of female of *Colias philodice* from Hanover, N. H., resembling *C. nastes* of Labrador, shown in the lower figure.

color, potentially white, though modified probably by the effect of cold upon the chrysalis in early spring into a form strikingly like that of the Arctic species, *Colias nastes*. I hope to ascertain from caterpillars now hibernating whether this spring form may be produced at will from larvæ from a white mother by the action of cold upon the chrysalis.

My attention was attracted to the problem of inheritance of the white color in this species by certain statements in Edwards's great work on the "Butterflies of North America." He says that the progeny of an albino female are partly albino and partly yellow, or it may be all yellow. "In one instance," he says, "I had five butterflies from eggs laid by an albino, and there resulted one male and four yellow females, no albino.

In another case of four females one was an albino. Mr. Mead has met with similar results, and neither of us have known an albino to be produced from the eggs of a yellow female." These brief notes pointed

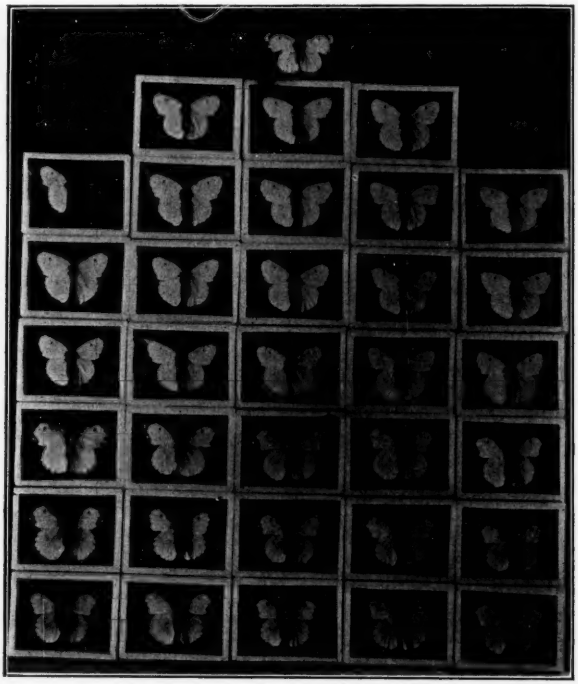

FIG. 5. The spring form of female of *Colias philodice* (at the top) and her offspring. The two rows at the bottom are yellow females; the third row from the bottom are white females. None of the offspring resemble their *nastes*-like mother.

so clearly to Mendelian inheritance that I resolved to investigate the matter, and I have thus far bred over 900 individuals from white females and from the daughters and sons of white females. In general my results differ from Edwards's observations at two points: (1) The white females always produce both white and yellow females, provided the family is large enough to represent all the possibilities. The family mentioned by Edwards, four yellow females, no white, was too small to indicate

that the mother would produce no white offspring. (2) Yellow females under certain conditions do produce both yellow and white offspring. Thus the mothers of families "e," "f," "i," and "k," 1910, were yellow, producing, respectively: 13 white and 14 yellow daughters; 7 white and 5 yellow; 30 white and 14 yellow; 19 white and 19 yellow. The conditions under which these four yellow females produced white offspring were alike. The female and the brother with which she mated were in each case the immediate offspring of a white female, the male mate in each case being presumably heterozygous for color, y(w), the yellow female homozygous for that color, yy.

1. Inheritance of the White Female

Summary of Results

My observations, begun in the fall of 1908 and extending through the two following seasons, some of the same stock now being in hibernation, may be summarized as follows:

1. The white female, of which I have tested 13 individuals, is in all cases heterozygous for color, producing when crossed with a pure yellow male (wild, or her own brother), either equal numbers of white and of yellow female offspring, in accordance with Mendelian expectation (stock from Cambridge, Mass., families a, b, c, d, 1910), or twice as many yellow females as white (stock from Hanover, N. H., families a and c, 1909). The male offspring of a heterozygous white female are all yellow, though presumably one half are heterozygous, y(w), and one half homozygous dominants, yy.

2. It is evident from these observations that white is dominant in the female, yellow in the male, these being the colors of the respective heterozygotes. This case is comparable to the results obtained by Wood in crossing horned Dorset with hornless Suffolk sheep, the male heterozygote of F_1 having horns, the ewes being hornless. The horned condition is therefore dominant in the male, while in the female hornlessness is dominant.

TABLE I

WHITE ♀[4] [HETEROZYGOUS, W(Y)] × YELLOW ♂ [HOMOZYGOUS, YY]

Mother	Father	Name of Brood	Number of Males	White Females	Yellow Females
Wild, white	Wild, yellow	1808	3	2	3
" "	" "	1909 a	39	7	16
Nastes-like form[5]	" "	" b	19	5	10
Wild, white	" "	" c	13	3	7
Total in 1908 and 1909			74♂♂	17♀♀	36♀♀

Mother	Father	Brood	Males	White Females	Yellow Females
Wild, white A	Wild, yellow	1910 a	18	6	9
" " B	" "	b	79	22	28
" " C	" "	c	24	8	8
" " D	" "	d	30	15	13
Total in 1910			151♂♂	51♀♀	58♀♀

3. If a heterozygous white female is crossed with certain other yellow males, her brothers and the sons of the same white female, that are heterozygous for color (as indicated by the fact that when mated with homozygous yellow females both white and yellow offspring result), a larger number of white females than of yellow are produced, though not three white to one yellow according to Mendelian expectation. The proportion observed is approximately two to one (viz., 38:22, 13:8, g and h, 1910, and probably the 8:4 of family 2w, 1909). This proportion may be explained, as Dr. Castle first suggested to me, by assuming that in these families no homozygous whites occur, through infertility or abortion of the "white" germ cells that would naturally combine with white, so that the offspring consist of:

♂♂ 25 per cent. homozygous yellow, yy, and 50 per cent. heterozygous yellow, y(w).

♀♀ 25 per cent. homozygous yellow, yy, and 50 per cent. heterozygous white, w(y), no pure homozygous whites of either sex occurring in my cultures.

[4] The sign ♀ stands in Tables I–VI for the white female, ♀ for the yellow female.

[5] This individual is possibly a pure yellow (yy) ♀, modified by cold and mated with a heterozygous y(w) male. It is possible that this brood should be included in Table IV.

TABLE II

WHITE ♀ [HETEROZYGOUS, W(Y)] × YELLOW ♂ [HETEROZYGOUS, Y(W)]

Mother (white)	Father (yellow)	Brood	Males	White Females	Yellow Females
$1d^{36}$	*$1d^{8}$ ♂	l	4	3	3
$1d^{39}$	†$1d^{18}$	g	63	38	22
$1d^{45}$	"	h	16	13	8
Total			83 ♂ ♂	54 ♀ ♀	33 ♀ ♀

TABLE III

WHITE ♀ [HETEROZYGOUS, W(Y)] × YELLOW ♂ [UNTESTED, YY OR Y(W)]

Mother (white)	Father (yellow)	Brood	Males (yellow)	Females (white)	Females (yellow)
a^{35} ♀	a^{6} ♂	1909, 2w	20	8	4
$4b^{21}$	$4b^{15}$	1910, m	9	5	3
$1b^{39}$	$1b^{31}$	o	9	3	4
Total			38 ♂ ♂	16 ♀ ♀	4 ♀ ♀

Thus here is a case comparable to that of yellow mice, which, as shown by Cuénot, Castle and others. are always heterozygous, homozygous yellow mice not being produced; so that the proportions obtained by mating yellow mice together is 66.6 per cent. yellow, 33.3 per cent. non-yellow.

4. The wild white males which occur rarely are presumably recessive homozygous whites, but none have yet appeared in my crosses of heterozygous yellow males with heterozygous white females (g and h, 1910), and I have not yet had an opportunity to test their possibilities in breeding.

TABLE IV

YELLOW ♀ [HOMOZYGOUS, YY] × YELLOW ♂ [HETEROZYGOUS, Y(W)]

Mother (yellow)	Father	Brood	Males	White Females	Yellow Females
a^{14} ♀	a^{7} ♂	1910, e	58	13	14
a^{10}	a^{19}	f	10	7	5
$1d^{30}$	‡$1d^{8}$	k	46	19	19
$1d^{46}$	‡$1d^{18}$	i	27	30	14
Total			141 ♂ ♂	69 ♀ ♀	52 ♀ ♀

*Tested by crossing with $1d^{30}$ ♀ (yellow). See Table IV.
†Tested by crossing with $1d^{46}$ ♀ (yellow). See Table IV.
‡See Table II.

TABLE V

YELLOW ♀ [HOMOZYGOUS, yy] × YELLOW ♂ [HOMOZYGOUS, yy]

Mother (yellow)	Father	Brood	Males	White Females	Yellow Females
a^{24}	a^{6}, a^{23}, a^{26} or a^{42}	1909, 2y	20	0	15

Total number of males 507
Total number of females 412

TABLE VI

THE RESULTS OF BREEDING EIGHT DIFFERENT PURE LINES OF STOCK DURING 1908–1910. Brackets enclose designations of individuals used in subsequent breeding

Mother	Father	Brood	♂♂	White Females ♀♀	Yellow Females ♀♀
1908					
Wild, white	Wild, yellow	.....	3	2	3
1909					
A ♀♀	" "	1909 a	39[a^{6}♂, *et al.*]	7 [a^{35}♀]	16 [a^{24}♀]
a^{35}♀♀	a^{6}♂	2w	20	8	4
a^{24}♀	Either a^{6}, a^{23}, a^{26} or a^{42}	2y	20	0	15
1909 B					
Nastes-like form	Wild, yellow	b	19	5	10
1909 C					
Wild, white	" "	c	13	3	7
1910 A					
Wild, white	" "	1910 a	18[a^{7}♂, a^{19}♂]	6	9[a^{14}♀, a^{10}♀]
a^{14}♀	a^{7}♂	e	58	13	14
a^{10}♀	a^{19}♂	f	10	7	5
1910 B					
Wild, white	Wild, yellow	b	79[$4b^{15}$♂, $1b^{31}$♂]	22[$4b^{21}$♀♀, $1b^{39}$♀♀]	28
$4b^{21}$♀♀	$4b^{15}$♂	m	9	5	3
$1b^{39}$♀♀	$1b^{31}$♂	o	9	3	4
1910 C					
Wild, white	Wild, yellow	c	24	8	8
1910 D					
Wild, white	" "	d	30[$1d^{8}$♂, $1d^{18}$♂]	15[$1d^{36}$♀, $1d^{39}$♀, $1d^{45}$♀]	13[$1d^{30}$♀, $1d^{46}$♀]
$1d^{39}$♀♀	$1d^{18}$♂	g	63	38	22
$1d^{45}$♀♀	"	h	16	13	8
$1d^{46}$♀♀	"	i	27	30	14
$1d^{30}$♀	$1d^{8}$♂	k	46	19	19
$1d^{36}$♀♀	"	l	4	3	3

If the proportion of yellow females to white is really greater in the spring brood than in those of summer and especially autumn, as Scudder states, then it would be evident that some of the yellow females of the spring brood are heterozygous for color. See p. 260.

5. Yellow daughters of a white female are probably all homozygous for yellow.[3] When crossed with certain of their brothers, presumably heterozygous for color, these yellow females produce both yellow and white female offspring, sometimes in equal numbers, in accordance with Mendelian expectation (broods e, f, k), but sometimes twice as many white as yellow (brood i).

6. Yellow homozygous females, daughters of a white female, when mated with other brothers presumably homozygous produce only yellow offspring (brood 2y, 1909).

2. Inheritance in *Colias Edusa*

The numbers of typical orange and of white females of the European *Colias edusa* obtained by Frohawk (1901) from the eggs of four wild white females (var. *helice*), viz., 110 white ♀♀ (*helice*) and 125 orange ♀♀ (*edusa*) with 302 ♂♂, are in approximation to equality, and point to the conclusion that, in this species also, the white female is heterozygous for color.

Harrison and Main (1905) raised from the eggs of a white female (*helice*) of this species 79 ♂♂, 52 ♀♀ *helice* (white), and 19 ♀♀ *edusa* (orange). The numbers indicate that in this case both the parents were probably heterozygous for color. All the male offspring were of the typical orange hue, so it may be assumed that the 25 per cent. of homozygous white males that would be expected from mating two heterozygotes together were aborted, though the numbers indicate that 25 per cent. of the females were homozygous in whiteness. The expectation in the distribution of the observed number (71) of females would be

[3] It is of course not impossible that yellow females that are heterozygous for color may exist, and that this may account for the excess of yellow females over white in broods a, b and c, 1909. In order to test this matter and to determine whether, when a pair of yellows throw white, it is the male or the female that carries the white, the male crossed with any yellow should first be mated with a female known to be of a pure yellow strain. If such a pair throws only yellow, he is of course pure yellow, and if he is then paired with a yellow, and white offspring should appear, the occurrence of a yellow heterozygous female would be demonstrated, but if he has produced white offspring with a pure yellow female, he is assuredly a heterozygote, and will have some white daughters when paired with any yellow female.

$17\frac{3}{4}$ homozygous white, ww, $+35\frac{1}{2}$ heterozygous white, w(o), $+17\frac{3}{4}$ homozygous orange, oo, $=53\frac{1}{4}$ white [ww $+$ w(o)] $+17\frac{3}{4}$ orange, which accords closely with the actual count, viz., 52 white (*helice*), 19 orange (*edusa*).

3. General Observations on the Genus *Colias*

Since the female color pattern is the one that prevails in both sexes when there is no differentiation (*e. g., Colias nastes, C. hyale,* etc.) I am inclined to the view that in this genus of butterflies at least, as probably in birds, the secondary sexual characters of the male represent a more highly modified, those of the female a more primitive, condition. We may recognize in this country, as in the eastern continent, a natural series of species of the genus *Colias,* at the beginning of which stands the undifferentiated Arctic *Colias nastes* of Labrador, Greenland, northern British America and Alaska, with the female color pattern, and a dull greenish yellow ground color suffused with brown, common to both sexes. This ground color, as my brood of *Colias philodice,* 1909, b, shows, is closely related to white and probably interchangeable with it. Next in the series are the subarctic *C. pelidne* and *C. scudderi,* in the males of which the yellow color and black color pattern typical of many species of *Colias* attain their full development, while all the females are clear white, with faint marginal dark bands.

The yellow ground color and the solid black marginal band probably arose by mutation in an undifferentiated *nastes*-like or white stock, and at once became dominant in the male, while the original colors and color pattern remained dominant in the female.

Southward from the range of *C. pelidne,* in the Canadian faunal region, is the closely related *C. interior,* in which yellow females (var. *laurentina*) occur, though white females are "on the whole commoner" according to Scudder, and from this region southward extends *C. philodice,* in which the yellow females generally are far more adundant than the white. Finally, the orange color of *C. eurytheme* of the central and western states, in

which species a most complicated polymorphism occurs, probably represents a stage in evolution beyond the yellow, as does also the black of the melanic male mutant of *Colias philodice.*

The view that the color and color pattern of the male butterfly diverge more widely from the typical coloration of the group to which the species belongs, than those of the female, though advocated by Darwin, 1871, was strenuously opposed by Scudder ('89, Vol. 1, p. 531), who cites the white female of *Colias philodice* as evidence to support his position. The case of *Argynnis diana,* in which the dark blue female differs much more widely from the usual tawny color of the fritillaries than does the male, certainly points strongly to Scudder's view, but it may well be that no one rule applies to all genera of butterflies, though there are in butterflies and in birds few if any exceptions to the law that the plumage of the male is more brilliantly colored and more highly differentiated than that of the female.

4. Inheritance in *Papilio memnon*

Jacobson's observations on the Javan butterfly *Papilio memnon,* in which there are three varieties of female, and the discussion of them by de Meijere, 1910, show that, as in *Colias,* the dominant form among the females is the one most unlike the male, viz., the brownish, tailed *Achates;* the form that is recessive in the female, as in *Colias* also, is the one most like the male, viz., the dark tailless *Laocoon.* The intermediate variety, *Agenor,* is heterozygous, epistatic to *Laocoon* but hypostatic to *Achates.* In the male the dark color, recessive in the female, is completely dominant.

Inspection of Jacobson's results leads one to believe that two, or probably three, pairs of unit characters are involved, and that not all of the individuals recognized as *Achates* or as *Agenor* are of the same gametic constitution. The remarkable fact brought out by Jacobson is that, in the various combinations made, only two of the three varieties of female were obtained in any one brood.

As a working hypothesis, I regard the dominant female

form (the brownish tailed *Achates*) as the original type, from which the tailless dark-colored male and the somewhat similar *Laocoon* have been derived by mutation, in the same way that the white color, dominant in the female but recessive in the male of *Colias,* may be postulated as the ancestral color in that genus.

5. Inheritance of Sex

Discussion of the inheritance of sex in *Colias philodice* at present must deal in part with unverified hypotheses, because I have not yet secured and tested white males nor, if they exist, homozygous white females. Since, however, all other possible combinations have been realized, these may now be reviewed, and tentative predictions made as to what progeny may be expected in the future from homozygous white stock in its various combinations.

Let us suppose that the male color pattern and all primary and secondary sexual characters of the male are dependent upon the presence of a "determiner" for which the male individual is a homozygous dominant (xx), while the female individual is heterozygous, one half of the gametes which it produces containing the determiner (x) and one half lacking it (o). Thus the gametic constitution of the female may be represented as xo, that of the male as xx.

Taking color into consideration, the nature of the pure yellow male may be represented by the symbol: yyxx, that of the pure yellow female as yyox. Furthermore, if yellow is dominant in the male, and white in the female the male heterozygote would be y(w) xx, while the white female would have the symbol w(y) ox. Such a white female, being heterozygous in both color and sex, may be further assumed to produce in equal numbers gametes of four kinds. This hypothesis will appear perhaps more firmly grounded if we imagine that both of the mitoses which give rise to the polar bodies are differential divisions, instead of one being an equation division and one a differential division, as is usually as-

sumed or demonstrated to be the case. The eggs of the white female are, accordingly, to be represented as follows: yx, yo, wx, wo; those of the yellow female: yx and yo. It is not necessary to assume in gametogenesis of the heterozygous white female of *Colias* any repulsion between one determiner and another resulting in a coupling such as is believed to occur in *Abraxas*. The determiner for yellow and that for white have equal chances of passing into a gamete with the male determiner or into one without it.

There are, of course, nine imaginable sets of combinations that would take place in the fertilization of the eggs of a species with three sorts of females: yyox, w(y)ox and wwox by the sperms of the males: yyxx, y(w)xx and wwxx. We will consider first the combinations that up to the present time actually have been made in my cultures.

1. THE PURE YELLOW FEMALE × THE PURE YELLOW MALE

yyox × yyxx

yx, yo = gametes of the female
yx, yx = gametes of the male

yyxx, yyox = 50 per cent. pure yellow ♂♂, 50 per cent. pure yellow ♀♀. (Brood 2y, 1909.)

2. THE PURE YELLOW FEMALE × HETEROZYGOUS YELLOW MALE

yyox × y(w)xx

yx, yo = gametes of the female
yx, wx = gametes of the male

yyxx, yyox, y(w)xx, w(y)ox

25 per cent. pure yellow ♂♂, 25 per cent. pure yellow ♀♀, 25 per cent. heterozygous yellow ♂♂, 25 per cent. heterozygous white ♀♀, all the males being yellow, and the females yellow and white in equal numbers. (Broods e, f, k, i.)

3. WHITE HETEROZYGOUS FEMALE × PURE YELLOW MALE

w(y)ox × yyxx

wx, wo, yx, yo = gametes of the female
yx, yx = gametes of the male

y(w)xx, w(y)ox, yyxx, yyox

♂♂ 50 per cent. pure yellow, 50 per cent. heterozygous yellow,
♀♀ 50 per cent. pure yellow, 50 per cent. heterozygous white,
all the male being yellow, the females yellow and white in equal numbers. (Broods a, c, 1909; a–d, 1910.)

4. WHITE HETEROZYGOUS FEMALE × HETEROZYGOUS YELLOW MALE

$\bar{w}(y)ox \times y(w)xx$

wx, wo, yx, yo = gametes of the female
yx, wx = gametes of the male

y(w)xx, w(y)ox, yyxx, yyox
y(w)xx w(y)ox

wwxx wwox. Assuming that the last two combinations (homozygous whites) are cancelled, we should have:
♂♂ 25 per cent. pure yellow, 50 per cent. heterozygous yellow,
♀♀ 25 per cent. pure yellow, 50 per cent. heterozygous white.
This combination has also been accomplished in my cultures, *e. g.*, broods g and h, 1910.

The five possible remaining combinations may never be completely realized owing to partial or complete infertility of the homozygous white stock. However, white males do occur, and assuming that homozygous white zygotes might be successfully produced, the resulting combinations would be as follows:

5. PURE YELLOW FEMALE × HOMOZYGOUS WHITE MALE

yyox × wwxx

yx, yo = gametes of the female
wx, wx = gametes of the male

y(w)xx, w(y)ox, that is, both males and females would be heterozygous for color, all the males being yellow, all the females white.

6. HETEROZYGOUS WHITE FEMALE × HOMOZYGOUS WHITE MALE

w(y)ox × wwxx

wx, wo, yx, yo = gametes of the female
wx, wx = gametes of the male

wwxx, wwox, y(w)xx, w(y)ox, giving

♂♂ 50 per cent. heterozygous yellow, 50 per cent. homozygous white,
♀♀ 50 per cent. heterozygous white, 50 per cent. homozygous white,
thus all the females would be white, but the males yellow and white in equal numbers.

7. HOMOZYGOUS WHITE FEMALE × PURE YELLOW MALE

wwox × yyxx

wx, wo = gametes of the female
yx, yx = gametes of the male

y(w)xx, w(y)ox, or the males all heterozygous yellow, the females all heterozygous white [the same result as in (5)].

8. HOMOZYGOUS WHITE FEMALE × HETEROZYGOUS YELLOW MALE

wwox × y(w)xx

wx, wo = gametes of the female
yx, wx = gametes of the male

y(w)xx, w(y)ox, wwxx, wwox, or
♂♂ 50 per cent. yellow, heterozygous, 50 per cent. pure white,
♀♀ 50 per cent. white, heterozygous, 50 per cent. pure white.

9. HOMOZYGOUS WHITE FEMALE × HOMOZYGOUS WHITE MALE

wwox × wwxx

wx, wo = gametes of the female
wx, wx = gametes of the male

wwxx, wwox, or the males all homozygous white, the females all homozygous white.

That the germ cells in the white female, which I have shown to be heterozygous for color, and which is presumably also heterozygous for the sex determiner, are really segregated in oogenesis into four distinct groups is strongly indicated by the realization of the results of this hypothesis as shown in ¶¶ 3 and 4. In this segregation there is no real "coupling," the sex determiner (x) being equally distributed among the white and the yellow gametes, but the chances are also equal that any gamete may receive the x factor, and become a male zygote when fertilized, or lack it, and become on fertilization a female organism.

As would be expected, there are similarities between *Colias* and *Abraxas*[6] in the method of inheritance of the white female variety in each. The female in both is heterozygous for sex, producing in equal numbers eggs which give rise to males and to females when fertilized by the like sperms of the homozygous male. But there are striking differences between the two forms in inheritance, *e. g.,* the dominance of the type color in *Abraxas,* compared with its dominance in the male only in *Colias,* white being dominant in the female; females of the type form that are homozygous for color are found in *Colias,* but not in *Abraxas,* in which all the type females are heterozygous, just as are all the white females of *Colias* that have hitherto been bred. The segregation of the

[6] Doncaster, L., 1908, Rept. Evol. Committee Roy. Soc., IV, p. 53.

color and sex determiners in the *grossulariata* female and the white female *Colias,* both of which are heterozygous in these two respects, takes place presumably by quite different methods. Other differences or similarities will doubtless come to light when the white male of *Colias* is bred.

The notation which I have here used to express the gametic constitution of *Colias* applies equally well to *Abraxas,* assuming that maleness is dominant and that in gametogenesis of the heterozygote for color and sex, viz., the female *glossulariata,* GLOX, the male determiner, X, accompanies into one gamete the determiner for high color, G; while the determiner for the undeveloped color, L, is coupled with that for the undeveloped (female) sex, viz., O. This seems to me to be a more plausible way of expressing the combinations demanded by the results than that there is a "repulsion" between the determiner for femaleness (which is assumed in this view of the case to be dominant) and that for the dominant strong color, G, as suggested by Bateson and Punnett.

On the other hand, it is true that their assumption that in *Abraxas* the male is a homozygous recessive may be applied equally well to *Colias.* However, I am constrained to adopt the view that the male in both is a homozygous dominant for the following reason:

Dominance in the male postulates the presence in all the sperms and in half the eggs of a chemical substance which in double quantity in an oosperm so stimulates it that the male characters, both primary and secondary, one by one make their appearance; while in single quantity (introduced by the sperm only) a lesser stimulus is given, and the organism develops in lesser degree along different lines into the female form. This hypothesis carries within itself an "explanation," feeble though it be, of the male form and color pattern, as well as of those of the female. It is in harmony with the fact that the intenser color of the male butterfly or moth, generally, represents a more advanced condition in the evolution of pigment than the paler colors of the female.

If, on the other hand, following the interpretation of

Doncaster's results given by Bateson and Punnett, 1908, and by Castle, 1909, viz., that the male is recessive and the sperms contain no sex determiner, which is presumed to be present in half of the eggs only, then we must imagine that a single quantity of this determiner raises one oosperm to the female condition, while, in the entire absence of it, it is understood that another oosperm proceeds to the development of the frequently more complex organs and generally brighter colors of the male.

In using a modification of the convenient notation for sex-limited characters devised by Wilson and modified by Castle to express the parallelism between recent discoveries in cytology and Mendelian segregation, I do not wish to imply that the symbol X, as applied to *Colias*, refers to any sort of chromosome. Nor is there, so far as I know, any cytological evidence as to the dominance or recessiveness of the homozygous male condition in the possibly large class of cases like *Abraxas* and *Colias* in which the female is presumably heterozygous for the sex determiner.

As Castle, 1909, has shown, there are two categories of cases in sex inheritance: viz., (A) those in which the female is assumed to be a homozygous dominant for the sex-determining factor (XX), while the male is a heterozygote, producing two sorts of spermatozoa that are not only physiologically but presumably even morphologically different. This category is illustrated cytologically by the extreme case of *Anasa*, in which one set of sperms, the male-producing, contain only four chromosomes each, while the other, the female-producing, have five, the number characteristic of all the eggs. The second class of cases (B) is that including *Abraxas* and *Colias*, in which the peculiarities of their inheritance can be explained by assuming that the female is heterozygous for the differential sex factor, producing two types of eggs, one destined, when fertilized by the sperm of the homozygous male to produce only males, the other only females. Furthermore Castle, following Bateson and Punnett, 1908, regards maleness as recessive, the oosperm contain-

ing only one sex factor, viz., that brought in by the spermatozoon.

The field represented by class A has naturally been well explored by cytologists, for in spermatogenesis the odd chromosome was discovered, and there it is expected; moreover the study of spermatogenesis is attended with less difficulty than oogenesis. Hence comparatively few observers have paid any attention to the behavior of the chromosomes in the maturation of the egg, and cytological evidence of the occurrence of possibly dimorphic eggs in the second class of cases is lacking, though Balzer's 1908 observations on oogenesis in the sea-urchin, mentioned by Wilson, 1909 b, indicate that something may be done along this line.

The cytological evidence bearing upon the Lepidoptera, so far as it goes, however, indicates that the male is morphologically homozygous. There is no dimorphism of spermatozoa, the same number of chromosomes being found in all the spermatids. There is, however, a heterochromosome, interpreted by the various observers as a pair of equal idiochromosomes, associated with the plasmosome in the growth period. According to Dederer, 1907, and Cook, 1910, it ultimately becomes indistinguishable from the other chromosomes, though in the butterfly and the moth examined by Stevens, 1906, its large size made it visible through the maturation mitoses, in both of which it divides into equal parts. Thus, in the seven moths and one butterfly (*Euvanessa antiopa*) examined by these observers, there is cytological evidence, if the chromosome theory of sex determination be assumed, that the male is homozygous. Unfortunately we have no exact information, so far as I am aware, as to oogenesis in butterflies. If it should be shown that in Lepidoptera there is a visible dimorphism of ova as regards the number of chromosomes, the cytological interpretation of sex determination would receive an interesting and important confirmation.

If such visible dimorphism should be discovered, it would be most interesting to see what bearing it has, if any, upon the question whether the homozygous male is

dominant or recessive. If the latter be indicated, then we may find that a suitable designation of the gametes of *Abraxas* and *Colias* would be that suggested by Wilson, 1909 b, viz., for the male YY and for the female XY, Y being the small synaptic mate of X, which is the large odd "female-producing" chromosome.

On the other hand, if the male is dominant a state of affairs that is exactly the reverse might be expected, viz., an absence of a chromosome, or an abnormally small one, in half of the eggs would be the visible sign of future femaleness. If these conditions should be realized, we might be able to identify the "equal idiochromosomes" already found in the spermatogenesis of butterflies with my XX of the male, the corresponding chromosome in the male-producing type of egg being X, the female-producing ova either lacking the chromosome altogether or having one of reduced size.

Dr. Castle, in a recent letter to me, expressed the opinion that the well-known anabolic tendency of the female, especially in reproductive activities, renders it extremely probable, on the other hand, that the female-producing gamete in every case of disparity should have the larger chromatic equipment. This seems to me very plausible, and it may well be that the findings of cytology in reference to this question can never do more than demonstrate the presence of this constant anabolic tendency in the female-producing gametes. The appearance of the large X chromosome in the female-producing gamete of the Hemiptera may be, therefore, only the visible expression of a sex tendency already established, as Morgan's observations on the cytology of *Phylloxera* indicate.

But the demonstration of this anabolic tendency, even in the unfertilized gamete, does not mean necessarily the *presence* of a sex determiner that is absent or deficient in the male-producing gamete, and hence the *dominance* of femaleness. It is just as reasonable to assume that the constant katabolic tendency of the male, evinced possibly by deficiency in chromatin at the start and certainly by the presence of horns, high colors and elaborate plumage

in adult life in many animals, is due to the excess of some hormone in a gamete which thereby becomes male-producing, in other words, to a *dominance of maleness.* On the other hand, in the absence of such an excitant, the recessive condition of femaleness would result, with a constant tendency towards quiescence, towards the accumulation of reserves of food to nourish the offspring, and the absence in the adult of the brilliant colors, horns and all the well-known and highly specialized secondary sexual characters of the male.

If it should be proved that maleness is dominant in lepidoptera in which the female is sexually heterozygous, may it not be true, on the other hand, that femaleness is dominant in the forms in which the male is heterozygous for sex, as in Castle's class A?

I see no inconsistency in these two antithetic categories, but should expect to find in the latter either that the female, and not the male, is the more variable, active and progressive, as in the bee, or that, as in hemiptera, both sexes are in external appearance and in habits much alike.

In brief, I have tried to point out in this discussion that a different interpretation from that of Castle may be applied to the case of *Abraxas,* and of *Colias* also, viz., that these cases, and others that may fall into the same category, differ from those of the well-established class A of Castle in that one is the exact reverse of the other, the female in class A being a homozygous dominant for the sex determiner, whereas in class B the male is a homozygous dominant, and not a homozygous recessive as has hitherto been assumed. The view here set forth not only accounts for the facts of Mendelian inheritance in these two insects equally as well as the other, but has the added advantage of harmonizing with the facts regarding the secondary sexual characters in lepidoptera and birds.[7] The high colors and elaborate plumage of the

[7] The recent experiments of Goodale, however, described in the *Biological Bulletin,* Vol. 20, No. 1, December, 1910, show that the removal of the ovaries from the Rouen duck produces a gradual tendency toward the assumption of the male plumage which is not in accordance with the view that

male are dominant characters eventually produced in the adult, according to my view, by the presence in the oosperm of a double quantity of a male-producing enzyme or similar substance. This hypothesis does not depend upon cytology for its support, though it is not impossible that future discoveries in oogenesis may be found to be in harmony with it.

6. Dimorphs

If complete separation of the yellow- and the white-bearing gametes should fail to occur in the oogenesis of the white female of *Colias,* in the differential division of an oocyte destined after fertilization to become a female individual, then the right wings of the future butterfly might be white, the left yellow, or *vice versa.* Such an individual, captured by Mr. J. H. Rogers, Jr., of Medford, Mass., is figured in *Psyche,* Vol. X, Pl. X, Fig. 4. A similar specimen of *Colias edusa,* the right wings being white, is figured by Fitch, 1878, in the *Entomologist* (No. 178, pp. 49–61). Fitch shows also a female with the fore wings white and the hind wings yellow. A gynandromorph might be produced by similar failure in the separation of a gamete containing the sex determiner from one lacking it. Various combinations of color and sex are theoretically possible in one individual, if we assume that imperfect division of the gametes may occur in gametogenesis. The discovery of these combinations in nature, or their production by artificial disturbance of the ova, is well within the limits of possibility.

The production of a dimorph with one side yellow and one white is easily explained if we assume, for example, that the determiners for yellowness and for whiteness, after synapsis, reside in a single bivalent chromosome, which fails to divide differentially in oogenesis, but passes over bodily into one of the gametes, the egg. If

the male in birds owes his more brilliant plumage to the addition of something to the female type.

the first cleavage completes the differential division of the bivalent chromosome, instead of dividing it lengthwise, the right and left dimorphism is easily understood. Or we might postulate the suppression altogether of the differential oogenetic division of the egg of a white heterozygous, w(y), female of *C. philodice* which normally results in the separation of color potentials, but it is questionable whether under such conditions the egg would develop.

Again, the theory of Boveri, 1902, that a gynandromorph is produced if a spermatozoon (sperm nucleus) unites with one of the two nuclei in the two-cell stage, instead of with the original egg nucleus; or that of Morgan, 1907, that two sperms enter, one uniting with the egg nucleus and (in the bee) determining the female half, while the other gives rise to the male half, may be applied to these dimorphs. According to Boveri's view, for example, we have to assume in the case of *Colias* that a "white" sperm from a heterozygous yellow male enters a "yellow" egg containing no sex determiner, and after awaiting the precocious division of the egg nucleus, unites with one of the two nuclei thus produced, and determines the character of the white, or hybrid, half of the resulting female organism.

7. Precocity of the Males

Males of *Colias philodice,* as in certain other lepidoptera, not only appear in the fields earlier than the females in the spring, summer, and autumn broods, but also, in every family of this species that I have raised, a very large proportion of males emerge from the chrysalis early in the period during which eclosion takes place. Thus, as shown by Table VII, in brood a, 1909, 28 males emerged from the chrysalis at the beginning of the period of eclosion, while only 3 females emerged during the same time, and, of the first half of the brood to pupate, 26 proved to be males and only 5 females. In general, 82 per cent. of the first half of the four broods for which data are here presented to reach the pupal

stage were males, only 18 per cent. females. The remaining individuals of these four families, constituting the second half of each in reaching the pupal stage, were, on the other hand, largely females (66 per cent.), only 34 per cent. being males.

These facts led me to entertain the idea that the eggs which are to become males may be laid before the female-producing ova. To test this hypothesis, I segregated the successive batches of eggs laid by seven females in 1910, and reared the larvæ of each successive batch separately, to see if the lots laid first by each female would contain a larger proportion of males than those laid later. It will be seen from Table VII that in families b, c, d and e there was in each case a slightly larger proportion of male eggs in the first laying than in the batches laid subsequently, but in families g, i and k exactly the reverse is true, the last lots of eggs laid by each female (viz., 3g and 4g, 2i, and 3k and 4k) containing more males than females. It is evident, therefore, that the male-producing ova are not laid on the average earlier than those that are female-producing, but that the larval period of the male is shorter than that of the female.

In consequence of this fact it is not surprising to find that when a brood of caterpillars is exposed to any adverse conditions such as starvation, an excess of male butterflies, as Mrs. Treat long ago found, will result, for the simple reason that many females, exposed to adverse conditions during a longer period of growth than that of the males, have been eliminated, while the more precocious male caterpillars survive in greater numbers. This will explain, I believe, the excess of males in my cultures, 507, or 55 per cent. of the total number being males, 412, or 45 per cent. being females. There is no evidence, however, of any differential death rate between the yellow and the white females. Neither is more precocious in larval development than the other, and intestinal diseases appear to strike each with equal virulence.

TABLE VII

PRECOCITY OF MALES IN *Colias philodice*

Year	Brood	First Half of Brood to Pupate ♂♂	♀♀	Dates of Pupation	Second Half to Pupate ♂♂	♀♀	Dates of Pupation	First Eclosion ♂♂	♀♀
1909	a	26	5	June 25–29	13	18	June 29–July 1	July 2–9 28	3
1909	b	14	3	July 2–4	5	12	July 4–6		
1909	c	10	1	July 7–10	3	9	July 11–13		
1910	a	13	4	July 9–13	5	11	July 13–19		
	Total	63 ♂♂	13 ♀♀		26 ♂♂	50 ♀♀			

Eighty-two per cent. of first half of all broods in reaching the pupal stage are males.

Thirty-four per cent. of the second half of broods in reaching the pupal stage are males.

Year	Brood	Males	Females	Per Cent. of Males	Brood	Males	Females	Per Cent. of Males
1910	1b	33	12	73 from 1st batch	1g	16	13	55
	2b	7	3	70 from 2d batch	2g	18	23	44
	3b	9	7	56 from 3d batch	3g	21	19	52.5
	4b	30	28	51.7from 4th batch	4g	8	5	61.5
	1c	20	13	60.6	1i	13	22	37
	2c	4	3	57	2i	14	22	38.8
	1d	12	10	54.5	1k	8	11	42
	2d	7	6	53.8	2k	15	12	55
	3d	11	12	47.8	3k	13	10	56.5
					4k	10	5	66.6
	1e	13	3	81.2				
	2e	18	12	60				
	3e	27	12	59				

These investigations are by no means finished, and any one who should chance to capture any unusual specimen of this species, or of any closely allied to it, showing melanistic or other aberrant tendencies, would confer a great favor on the writer of this paper by mailing to him the specimen alive in a metal box lined with moist filter paper sewed firmly against the perforated sides. A white male is, of course, especially desired.

In conclusion, the writer wishes to express his hearty thanks to his friend Mr. P. W. Whiting, an accomplished student of butterflies, for his kind and efficient cooperation in the field work connected with these studies and in the laborious processes of preparing specimens for detailed examination. The friendly counsel of Dr. W. E. Castle has been also of great value to the writer in

entering this to him new but extremely fascinating field of investigation.

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NUCLEUS AND CYTOPLASM IN HEREDITY[1]

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THAT there is a physico-chemical basis of heredity and that it is, if not exclusively, at least fundamentally bound up in the proteins of the germ-cells, we know for certain. If there is anything else than this physico-chemical basis we do not know it. But even should there be, it is inconceivable that it is not subject to physico-chemical agencies and limitations, and we are bound, therefore, to continue our search for these material factors as long as we can unearth new facts or arrive at new generalizations.

Before undertaking a discussion of the germ-cell, however, I wish to call attention to certain chemical facts that are frequently overlooked or slighted by the biologist.

In chemical reactions we have not only to take into account the initial chemical substances and such external factors as pressure, temperature, etc., but in many instances we must reckon also with the quantitative relations, especially the concentrations of the various substances, and the velocities of their reactions, since alterations in either of these factors may profoundly modify the end-products of the reactions. A very simple example of quantitative relations is seen in the combination of carbon and oxygen. If much oxygen is present, CO_2 is formed, if little CO, and these are two very different substances, particularly when physiologically considered. Or, when chlorine acts upon methane, CH_4, depending upon purely quantitative relations and physical conditions, any one of four different substitution products ranging from CH_3Cl to CCl_4 may be secured.

The questions of quantitative proportions and of velocities are of especially great significance in a sequence of

[1] Read before the American Society of Naturalists, at Ithaca, December 30, 1910.

reactions where a number of associated substances are concerned and where certain of the materials, before they can become active, must await the outcome of the reactions between other members of the mixture. For example, when hydrochloric acid is passed into an alcoholic solution of hydrocyanic acid, provided there are sufficient quantities of these three ingredients, five definite crystalline end-products of their interaction result. First the hydrochloric and hydrocyanic acids combine to form amido-formyl-chloride, which then adds another molecule of hydrocyanic acid. This product next reacts with one molecule of alcohol which to this point has been inactive. The result is what we may call end-product one. Then end-products two, three and four, respectively, are formed by the successive additions of a single molecule of alcohol to separate molecules of a part of the immediately preceding end-products. The fifth end-product is not so directly related to the others. It is elaborated chiefly through the interaction of hydrocyanic acid and water, but this interaction can not take place until water is released through dehydration of some of the other compounds. There is little doubt that such sequential reactions as these may be taken as simple models of what goes on on a tremendous scale in the developing germ-cell.

It is a well-known chemical fact, moreover, that when two or more progressive reactions are going on simultaneously, a quickening or retardation of the velocity of either, with the consequent precocious development of certain stages in the sequence, may lead to a partial or complete deflection of the original trend of the reactions and the formation of entirely different end-products than would otherwise have resulted. And velocities may be varied greatly by such factors as temperature and catalytic agents.

But what has all this to do with the germ-cell? Simply this, the substance of the germ-cell, in so far as we know it, is of materials such as proteins, carbohydrates and fats which we have no reason for doubting are subject

to the same fundamental laws of chemical behavior whether they exist in living matter or in non-living matter. If in the comparatively simple cases of associated simultaneous reactions with which we are acquainted in non-living matter, relative velocities may so modify the results, we can readily realize of what tremendous importance regulation of this matter must become in living protoplasm where doubtless vast numbers of chemical reactions and interactions are going on at the same time. In fact, could we locate such a time regulating factor in the germ-cell it would seem that we had accomplished a long stride toward an understanding of the controling and coordinating mechanism which insures the appearance of just the proper substance at the right time in morphogenesis. It would constitute a qualitative as well as a quantitative regulator, for by determining quantity at any given time it determines what the next chemical reaction will be, and hence in the very doing of this, it necessarily conditions the chemical outcome of that reaction. As we have seen, temperature and catalytic agents are important factors in modifying the velocities of reactions in ordinary chemical processes, and inasmuch as under normal conditions of development the temperature factor is a fairly constant one, we are left to face the question as to whether in protoplasmic phenomena there is anything to correspond to catalyzers. Such substances we find in the enzymes.

While the method of enzyme activity is not positively known, the consensus of opinion of those who have studied them most seems to be that they act by catalysis. For instance, both catalyzers and enzymes are effective in very minute quantities; neither appears among the end-products of the substances acted upon, but exists independently and in exactly the same quantity as at the beginning of the reaction; external conditions such as temperature affect their activities similarly; and lastly, the rate, that is, the velocity of the reaction concerned, depends upon the amount of the catalyzer or enzyme present. When we have explained the phenomena of

catalysis, therefore, we have at the same time doubtless gone far toward explaining the action of enzymes.

We know that different ferments act differently on the same substance and that the same ferments may act on different substances within certain limits. To realize the truth of the first proposition we have only to compare the results of the butyric, the lactic and the alcoholic fermentations of grape sugar. As to examples of the same ferment acting on different substances, we may point to the fact that some varieties of yeast will act readily on *d*-fructose, *d*-glucose, and *d*-mannose. They will not act on *d*-galactose, however. Furthermore, none of the other known aldose hexoses and ketose hexoses are acted upon by yeasts. In the case of yeast, then, where a given enzyme acts on more than one substance, the molecular configuration of the respective substances must be closely similar. This seems to be a general rule. We do not find the proteolytic enzyme trypsin attacking anything but proteids, although it operates on different kinds of proteids. Even oxidizing ferments are not exceptions in this respect, for certain of them will yield oxidations in some compounds and not in others that are readily oxidizable under the influence of a different oxidizing ferment.

But granted that in living protoplasm ferments play the important rôle of velocity regulators and consequently of conditioners of both quantitative and qualitative results, where should we look for them in the germ-cell? It is now a matter of common knowledge that probably many ferments are closely associated with nuclear activity and presumably originate within the nucleus. The present tendency is to regard the dissolution of the nuclear membrane from time to time as a means of distributing substances to the cytoplasm. Particularly in the case of the germinal vesicle of the egg, upon dissolution of the membrane, there is a copious discharge of nuclear material into the cytoplasm, and one would naturally infer that this is in some way a preparation for the subsequent rapid differentiation which will occur.

Various observers have pointed out the predominant part played by the nucleus in intra-cellular oxidations, operating apparently by means of oxidases. R. S. Lillie has shown that in the indophenol reaction the colored oxidation products in such cells as red corpuscles, and those of liver and kidney, are deposited mainly in and around the nuclei. He further points out[2] that certain ferments exhibit the properties of nucleoproteids and that they are apparently concerned with later chemical changes in the protoplasm chiefly oxidative in nature. As far back as 1895 Wilson and Mathews[3] showed that in the first maturation division of the starfish egg much chromatin is set free in the cytoplasm. In 1902 Conklin[4] called particular attention to the escape of nuclear material into the cytoplasm upon dissolution of the nuclear membrane in the egg of *Crepidula,* remarking further upon the large proportion of chromatin that passes into the cytoplasm during every cell cycle, where seemingly it plays some important part in the subsequent changes of the latter. Likewise, F. R. Lillie,[5] in 1906, pointed out that an important part in the development of *Chaetopterus* is played apparently by the great quantities of a "residual substance" set free from the germinal vesicle. Lyon[6] in 1904 showed a rhythmic parallel between nuclear division and the production of carbon dioxide by the cleaving egg. And Mathews[7] in 1907 suggested as probable that the periodic disappearance of the nuclear membrane during mitosis brought about a distribution through the cytoplasm of oxidases which had been synthesized in the nucleus. Wieman[8] in 1910 has shown the existence of alternate phases of acidity and basicity in the process of yolk formation in *Leptinotarsa,* due to a succession of oxidation processes which occur in

[2] *Jour. Exp. Zool.,* Vol. V, pp. 379–428, 1908.
[3] *Jour. Morph.,* Vol. X, pp. 319–342, 1895.
[4] *Jour. Acad. Nat. Sci., Phila.,* Vol. XII, pp. 1–121, 1902.
[5] *Jour. Exp. Zool.,* Vol. III, pp. 163–268, 1906.
[6] *Am. Jour. Physiol.,* Vol. XI, pp. 52–58, 1904.
[7] *Am. Jour. Physiol.,* Vol. XVIII, pp. 89–111, 1907.
[8] *Jour. Morph.,* Vol. XXI, pp. 135–216, 1910.

the basic-staining food-stream as the result apparently of the discharge of oxidase from the nucleus into the cytoplasm of the egg. Again, it is of great significance that in the embryos of seeds the time of greatest fermentative activity in starches and other fermentable bodies coincides with that of maximum size of the nuclei. Many other significant facts might be adduced, but I wish merely to show that there is abudant evidence pointing to the nuclei of cells as sources of enzymes.

The idea that among other things the nucleus is concerned with enzymic activities in the cell, or, indeed, that the chromosomes themselves are sources of ferments, is by no means a new one. The last few years has seen a steadily increasing tendency to regard them as such. The latest and most outspoken suggestion of this nature, of which I am aware, is the argument that Montgomery,[9] brings forward in a recent paper. He says in part, "The relative constancy of chromatin mass in spermatocytes and spermatids of very different volumes speak strongly for its enzyme nature." Then after pointing out the relative constancy in size between the univalent components of spermatogonia and spermatocytes in *Euschistis* and reminding us of the well-known fact that, although the egg is many times greater than the sperm, the chromosomal contribution of each is the same in size and mass, he goes on to say that, "An enzyme possesses among other properties the power of engendering changes in its medium while still preserving a constant mass." And he continues, "Of all the larger cellular compounds that we know, the chromosomes agree most closely with this definition, and by reason of this constancy of mass alone might be considered enzyme masses."

My present thesis, however, while in harmony with all this, is yet different. It is rather just the complement of such a proposition as Montgomery's for it is an attempt to show reasons why there *must* be a nicely adjusted series of such substances in the germ-cells as enzymes.

In any epigenetic conception of the germ-cell—and this

[9] *Biol. Bul.*, Vol. XIX, pp. 1–17, 1910.

in greater or less degree seems to be the only plausible one to-day—we are forced, in explaining morphogenesis to postulate the existence of some time-, quantity- and quality-controlling mechanism. The one evident class of substances in the germ-cells which can fulfil the necessities of the case are the ferments. For since they will determine the velocities of chemical reactions they must in consequence control the quantitative relations of the cell chemistry at any given unit of time. But from the very fact that where a large number of associated reactions are going on simultaneously, these quantitative relations at given stages of the chemical interchanges must profoundly influence qualitative results, we can not but conclude that this initial control of velocities must condition the qualitative results.

If we regard the chromosomes as centers of such a series of velocity-controllers, or, in other words, as sources of various enzymes, we can at once appreciate the necessity for having them so accurately balanced off in size and particularly in their quantitative relations one to another. For since the velocity of the reaction in a fermentable substance is determined not only by the presence of the ferment, but also by the amount of it, the quantitative relations of the ferments to one another would have to be very accurately maintained.

What appears to be in a way a non-chromosomal demonstration of this fact is found in connection with the chloroplasts of plant cells which seem to exercise their functions at least in part through the agency of ferments. As is well known, in cell division these bodies are each carefully divided and handed on to the daughter cells so that a constancy in number and in general relationships is maintained.

But, it may be objected, what is to be done with those cases of nuclear division in which the mitotic divisions of the germ-cells have been preceded by a series of amitotic divisions? Wieman[10] has shown that in amitosis the appearance of the division figures is by no means the

[10] *Loc. cit.*

same in all cases and that where it occurs among germ-cells the mechanism is more carefully adjusted than elsewhere. To quote his own words regarding such divisions in *Leptinotarsa*, "Thus in the oögonia and spermatogonia, division of the nucleus is preceded by a very exact division of a large chromatin nucleolus, and as the halves separate surrounded by a clear area, the appearance reminds one very much of the division of a chromosome on a spindle." Other investigators of such amitosis depict in their figures a mechanism which may have the same significance. From preparations of my own showing amitosis in the testes of snails and of *Planaria*, a similar interpretation could be given.

On this enzyme conception, however, constancy in number is not the fundamental necessity. The requirement is really constancy of equilibrium between chromosomal constituents. It matters not whether this is maintained in sixteen, eight, four or one chromosome, so long as the balance between the various enzymic foci, or the capacity for the restoration of such a balance, is maintained. The ultimate karyokinetic divisions of such germ-cells as earlier divide amitotically would seem to be the restitution of such a balance so that the proper quantitative conditions exist in the finished germ-cell. Wieman would account for the appearance of amitosis in early germ-cells on the ground of a reduced oxygen supply in each individual cell, consequent upon a very rapid increase in cell multiplication. All that is demanded in the enzymic conception which I am presenting is the preservation in some way of the general tension of equilibrium so that each enzymic focus can resume its customary activities when the occasion demands, or, to express it less teleologically, when the occasion permits.

This conception would seem all the more tenable since we have had to discard the idea of the continuance of actual chromosomal individuality in favor of that of their genetic continuity as expressed by Wilson. The

demonstration by Bonnevie,[11] that while the identity of the old chromosome is lost in the resting nucleus, nevertheless, each new chromosome arises by a kind of endogenous formation from within the substance of its immediate predecessor, is a good point in evidence. That mere number of chromosomes is not of fundamental importance is evidenced by the considerable number of known cases in which closely related species may be characterized by a considerable difference in the number of chromosomes. In my own researches on man and certain birds, I have shown that instead of eight, the expected number of chromosomes in spermatocytes of the second order, only four (disregarding the accessory which may be present) appear, but that they are apparently bivalent in nature.

As associated with embryonic development we should have to suppose that there are considerable numbers of these initial ferments, which, however, need not all be present in an active condition. Certain ones required for the first stages of development might well be supposed in the course of their activities to produce or free others, or activate them at the proper time to take up their part in the progressive chemical activities of development. It is probable, too, that many of the ferments of the fully developed organism peculiar to the special tissues have not existed as such in the germ-cell at all, but have arisen at a later stage in the cells they occupy as the outcome of the metabolic activities of the tissue cell itself. It is a current belief, indeed, that each kind of cell has its own specific ferments whereby it shapes up from the common food supply submitted to it in the lymph the substances necessary for its own intramolecular assimilation. Many intracellular enzymes are now known to exist and it is probable that proteolytic enzymes at least are found within the cells of all living tissues. This is demonstrated by the fact of autolysis, or the self-digestion of living tissues which

[11] *Arch. Zellforsch.*, Bd. I, pp. 450–514, 1908.

have been taken from the body under perfectly aseptic conditions and kept suitably warm and moist.

There is no obstacle in the way of supposing, furthermore, that if we regard ferments as of nuclear origin, the cytoplasm of a given tissue may not modify the ferment, as it itself takes on the necessary modifications for its own specific functions. We have good evidence that the production of ferments can be modified by even the substratum on which living organisms grow, and such a relation as this, close as it is, is certainly less intimate than that existing between nucleus and cytoplasm. For example, molds cultivated upon starch form diastase, but if provided with albumin they will produce instead a proteolytic ferment. Moreover, by gradually altering their other nutriments, yeasts can be made to utilize after a time various foreign compounds.

But granted the necessity of some such set of controllers as the enzymes, and locating them in the chromosomes of the germ-cells, does this not commit us to a rigidly chromosomal theory of heredity? By no means. If, as all evidence indicates, ferments operate as catalyzers, then we must not forget that it is the very general belief among chemists that catalytic agents do not initiate the chemical reactions with which we find them associated, but that they only tremendously accelerate such reactions, or in a few known instances retard them. Since the nature of the building material must determine fundamentally the nature of the thing built, we must look outside the enzymes for much that will determine the peculiar individual outcome of the developmental processes. Leaving out of consideration for the present other functions the chromosomes may subserve, we might regard them as a sort of gauge for the feeding out of enzymes at the proper rate to bring about proper velocity reactions in the other cellular constituents, and perhaps regard the whole matter of mitosis and exactness in chromosomal distribution as a mechanism by which a quantitative metabolic regulation is maintained.

But because chromosomal influences can regulate the

activity of other cellular constituents, there is no warrant for jumping to the conclusion that they are essentially more important than these other constituents. I may repeat in this connection what I have had occasion to say by way of reminder in a former paper, "A germ-cell in fact should need no special units to generate the peculiar *genre* equilibrium or idiosyncrasy of protoplasm which is distinctive of a particular kind of individual, since such a germ-cell not only is itself already an individual, but from the very fact of having had the same racial history as other individuals of its peculiar kind (be they germ-cell, embryo or adult) it must likewise as a whole already possess this distinctive idiosyncrasy." That is, the individual proteids of germ-cells—globulins, albumins, nucleoproteids and the like—bear from the very start the stamp of individual peculiarity, wherever they may reside in the cell. And since they constitute at least part of the materials which transform and interact and have their actions modified by enzymes, certainly they as much as the enzymes are responsible for the outcome.

Regarding the specificity of corresponding proteins in relation to the natural kinships of living organisms, some very interesting facts are brought to light in the recent voluminous and painstaking researches of Reichert and Brown.[12] They show, for instance, that in hæmoglobin, one of the few crystallizable proteins, the crystals of each species of any genus, while possessing a constant individuality, all belong to the same crystallographic system and generally to the same crystallographic group of the system. These authors further point out the fact that this isomorphism must signify in all probability correspondence in the fundamental chemical constitution and molecular configuration of respective hæmoglobins. In case of the individual species the difference in the characters of the crystals was found to be as great as with ordinary chemical salts or minerals that belong to an isomorphous group. One is seemingly

[12] *Univ. Cincinnati Studies*, September–October, pp. 1–19, 1909.

justified, therefore, in inferring from these results that the differences between corresponding proteins in different species of a genus are rather to be referred to differences in molecular configuration than in atomic composition of the molecule.

The case of hæmoglobin is only one of several lines of evidence that might be brought forward as indicating the specificity of proteins. The serum-albumins which constitute the very font of the living molecules of higher animals, differ very decidedly in different species in the readiness with which they crystallize. Or, a foreign serum-albumin injected into the veins of an animal of different species can not take the place of the corresponding albumin of the blood of that species, but acts rather as a poison and is quickly eliminated by the kidneys. Lastly, not unduly to multiply examples of protein specificity, may be cited the precipitins which as you know may in general be used to show the degree of relationship of allied forms. For instance, when the blood-serum of one species of animal, let us say man, is injected at intervals into some other species, *e. g.*, the rabbit, the serum of the latter acquires the property of producing a precipitate in the serum of the first species, man in this case, but not in the serum of other animals unless they are relatively closely related to the first species. Thus the serum taken from rabbit's blood after a series of treatments with human blood will produce precipitation in the blood from any human being. It will produce some, though less, precipitation in the blood of the anthropoid apes, still less in monkeys, and none at all in animals distantly related to man. This implies, manifestly, that the more akin forms are, the more nearly identical are their proteins. And from the evidence brought forward in connection with the hæmoglobins we have seen that we are perhaps justified in regarding the differences between the proteins of closely allied forms as ones of molecular configuration rather than of molecular composition or constitution.

The question may arise in some minds as to whether

there could be sufficient number of configurational differences in the corresponding protein molecules of different species to account for the specificity of the respective proteins. When, however, we consider that to the serum-albumin molecule alone—and it is by no means the most complex protein—estimates assign the capability of having as many as ten thousand million stereoisomers, there would seem to be in this factor of configuration alone ample possibilities for the necessities of the case.

Because of imperfect methods it has in the past been well nigh impossible to tell how nearly chemically identical corresponding proteins of different species are. Reichert and Brown[13] point out that what formerly passed current as difference in composition may have been due in reality to contaminations or mixtures. "For instance," they go on to say, "the fact that the egg-white of the egg of certain species remains perfectly clear upon boiling, while that of other species becomes opaque, might be taken as meaning a difference in chemical composition, but the difference has been shown to lie in the different amounts of alkali and saline present." Again, "The centesimal analysis of corresponding albumins and globulins have failed to show any positive differences. Oppenheimer states, from the results of a recent study of serum-albumins of man, the horse and the ox, that serum-albumin is a uniform and specific substance, and that the elementary analyses point to one serum-albumin." This would leave the matter of specificity to be explained solely on the basis of molecular configuration.

This brings up the whole question of protein constitution and configuration. While this is still pretty much a terra incognita still many interesting facts have come to light, and all of them point to the conclusion that we are in no wise compelled to regard the proteins as out-

[13] "The Differentiation and Specificity of Corresponding Proteins and other Vital Substances in Relation to Biological Classification and Organic Evolution: The Crystallography of Hemoglobins," Publication No. 116, Carnegie Institution of Washington, pp. 1–338, 100 plates, 1909.

side the pale of the well-known principles of constitution, polymerization, stereometry and the like which are known to obtain in simpler organic compounds such as the "ring" compounds or aromatic series, and the straight chain or aliphatic series.

It is a familiar fact that the native proteins are readily broken down through hydrolysis into simpler bodies which still possess protein characteristics. We may in fact either artificially or in normal digestion get a whole series of stages ranging from complex native proteins to simpler and simpler products. The sequence runs approximately as follows:

Proteins.
—Meta- or infra-proteins.
—Proteoses.
—Peptones.
—Polypeptids (a relatively small number of amino-acids linked together).
—Individual amino-acids.

Three fourths of the albumin molecule, for example, may be made to yield members of the large group of amino-acids.

Because of the great abundance of these bodies, and because of their universal presence as degradation products of proteins, the conclusion was reached that the protein molecule is essentially built up by a linking together of amino-acid molecules. This suggested the idea that by bringing about such linkage it might be possible to build up molecules of the protein type. To those who are familiar with the recent developments of physiological chemistry, the fact that the first steps toward this end have already been accomplished is well known. Some seven or eight of the amino-acids (leucin, tyrosin, glycocoll, alanin, aspartic acid, phenyl-alanin, and amido-valerianic acid) had already been produced synthetically before Emil Fischer began his work. Fischer and his pupils have synthesized over twenty new members. But what is still more significant, they

succeeded in securing linkages of certain ones of these, thus producing polymeric amino-acid compounds called by Fischer polypeptids. Bodies of this same type have been isolated from natural organic substances. These polypeptids resemble peptones in appearance and, moreover, they react in the same way peptones do toward enzymes and various test reagents. One of the artificially synthesized polypeptids, furthermore, is apparently identical with one of the known polypeptids found in digestion, and *l*-leucyl-triglycyl-*l*-tyrosin, when prepared artificially, seems to have all the properties of the albumoses.

The amino-acids possess both acid and basic properties. It is this amphoteric condition that renders linkage possible. The individual amino-acids which constitute the units in such polymerizations are frequently spoken of as "nuclei." Linkage has been obtained not only between similar "nuclei," but also between "nuclei" of different amino-acids.

The results point clearly to the conclusion that the peptones and higher proteins are huge molecules formed chiefly of amino-acid molecules linked together by NH and CO affinities left unsatisfied as a result of processes comparable to dehydration. Such a protein molecule may perhaps be represented as a main chain or ring, of which the respective links are amino-acid "nuclei." Glycocoll, NH_2CH_2COOH, for instance, would through dehydration have for its nucleus in such a chain —NH.CH_2.CO—. Furthermore, since one H of the CH_2 of such "nuclei"

(*e. g.*, —NH.CH.CO—)
|
H

can be substituted by various compounds (acetic acid, buthane, methylparaoxybenzene, etc.) we are led to conclude that to each link of the protein chain, a side-chain, differing in constitution in different cases, is attached or is attachable by replacement of this hydrogen atom. The well-known instability of living protein would seem

to be due to the fact that the chemical systems in such a giant molecule are never fully saturated at any one time, so that there is continually an adding and detaching and shifting of side-chains with perhaps at times more fundamental shifts or replacements in the amino-acid "nuclei" themselves. Quantitative and qualitative differences of proteins would seem to depend fundamentally on the kind and amount of the constituent amino-acids and secondarily on the chemical nature of the various side-chains.

Probably the scheme as outlined is much simpler than the true conditions in the protein molecule, but it will serve as a sort of diagram of the relations which exist there. It is probable, too, that the conditions in different proteins vary greatly in complexity. The chief point to be emphasized is the fact that the results of many investigators bear out this general conception of the protein molecule.

It would seem then that in the light of our knowledge of the complex molecular configuration of the proteins, the substances which appear to be the most intimately concerned with life phenomena, we have, without resorting to the idea of mysterious separate entities, ample basis for that peculiar handing on of metabolic energies already established which we term *heredity*. The mechanism of heredity would seem to be not so much a local problem of nucleus or cytoplasm as of (1) fundamental species substances, probably mainly protein in nature, together with (2) equally specific enzymic substances which regulate the sequences of the various chemical and physical processes incident to development. As development progresses, more and more kinds of chemical products are released and in consequence an increasing number of chemical reactions are set going. After the germ becomes multicellular such new factors must be reckoned with as the influences, mechanical, chemical, etc., of the various parts of the body on one another. And even with our present meager knowledge of hormones we can see that this may be no inconsiderable factor in modifying the developing organs in complex organisms.

Looked at this way, the physical basis of heredity could not be considered a series of equipotent units, but rather it must be regarded as being composed of systems of units of different orders of organization and different degrees of coordination. Alterations in the configuration, constitution or relative positions of the unit constituents which represent the links of the main protein chain or ring, for instance, would precipitate much deeper-seated changes than would replacement of side-chains by those of different type, and such replacements would, in turn, doubtless appear objectively as differences of greater degree than those resulting from shifts in the composition or configuration of the individual side-chains.

Our whole scheme of natural classification, in fact, demands just such a physical basis as is depicted for the structure of the protein molecule. For morphological characters are not all equivalent. In any large group certain characters are more conservative than others and represent more fully the organization, as a whole, while in successive subsidiary groups the characters grade down to less and less inclusive ones until the trivial features which make up species differences and varietal traits are reached. However, this parallel between the make-up of the protein molecule and the natural classification of living organisms can be looked on only as a suggestive illustration because in addition to proteins other things often enter into the construction of what we term characters in plants and animals. These characters, indeed, are frequently blends of the effects of numerous influences.

But as an example of how changes in different parts of the protein molecule might work out visibly in the organism let us see how such alterations actually work out in simpler and better known compounds. In the familiar benzene ring compounds, for example, there exists (1) the main framework or more stable component, the so-called ring itself, and (2) innumerable substitution groups which can be attached to the "ring"

at any one of six places. These substitution groups can be shifted or replaced indefinitely without disrupting the ring itself. Still different effects are obtainable by the union of one or more rings (generally still retaining some of the substitution groups) directly with one another, or through the intermediacy of a third element or radical. In the numerous coal-tar colors, the color, which is one of the most obvious "characters," does not lie as such in the benzene ring itself, but is determined by the radicals attached to the ring, and in certain groups perhaps, in part by the manner in which two or more rings are united. If, for instance, into a molecule of azobenzene a radical of the amido-group (NH_2) is introduced, a body is constructed which through salt formation yields a dye. If instead of the amido-group a hydroxyl group is introduced, the result is likewise a dye but one of different color. And so a large series of tints may be produced by varying the substitution groups which replace H in the principal molecule.

We have constantly increasing evidence, finding recent expression, for instance, in a paper of Morgan,[14] of a fundamental stereometrical condition of the egg-plasm. And F. R. Lillie[15] has suggested the possibility that a specific polarity and symmetry are characteristic of the ground substance common to all cells of the organism. Stereochemistry is based on the assumption that the combining forces of an atom act in certain definite directions in space. This same conception of orientation must be carried on to the more complex organic units, the stereometrical relations of which, in turn, are but the continued expression, under other conditions, of the original atomic combining forces. And this being true, it seems reasonable to look upon the whole organism as but the further expression of such elemental factors.

In view of the facts regarding the closeness of identity of corresponding proteins of nearly related species, we must conclude that between two individuals of the same

[14] *Loc. cit.*

[15] *Jour. Exp. Zool.*, Vol. IX, pp. 534–655, 1910.

species, set apart by mere differences of sex and minor traits, the basal protoplasmic stereometry and the fundamental proteid constitution must be in large measure identical, so that bi-parental inheritance, if extending to all the details it has been assumed to embrace, would be largely a matter of duplicating identical protoplasmic constituents. It is an obvious fact, however, that the egg contributes vastly more cytoplasm than the spermatozoon, and in consequence the developing organism is more maternal than paternal in origin. I have argued this point at some length in a former paper,[16] where I attempted to show that we are not justified in asserting that the entire quota of characters which go to make up a complete living organism are inherited from each parent equally, but that rather we must restrict our assertion of equal inheritance to the sexual and specific differences which top off, as it were, the more fundamental organismal features. I further pointed out that since the actual manifest physical things contributed equally by each parent were the chromosomes, we might legitimately look to them as the chief source of the factors which determine individual differences. We know that a single reduced or haploid set of chromosomes is sufficient for normal development, both from the fact of artificial parthenogenesis, and the fertilization of non-nucleated egg fragments; hence the egg must contain all the possibilities of a new organism. But the only *measurable* things contributed by the sperm-cell are the individual characters of the male line.

We may infer then that the chromosomes of both male and female origin work together on or with the other germinal contents of the fertilized egg, and these are predominantly of maternal origin. Or to phrase it as I have in a former paper:[17] "Nevertheless, we can see how the veneer of individual traits may be equally of maternal and paternal origin if, to express it crudely, we look upon cytoplasm and chromatin, respectively, as responsive

[16] *Science*, June 28, 1907, pp. 1006–1010.

[17] *Univ. Cincinnati Studies*, September–October, pp. 1–19, 1909.

mechanism and inciting agent, the character of the response depending both upon the constitution of the cytoplasm and the material (enzymes? nutritive substances?) emanating from the nucleus."

If we consider that the supplying of the proper amounts and kinds of ferments is one of the important functions of the chromosomes, then we may suppose that in biparental inheritance each set of chromosomes is operating, probably catalytically, on a series of fundamental cell constituents that are largely common to both lines of ancestry; and that slight constitutional or configurational differences in corresponding enzymes bring about individual differences such as we recognize in the adult. We have already seen that different ferments within certain limits may act on the same substance and yield different results; consequently, in the intrusion into the egg of slightly altered enzymes in the chromosomes of the male, we should expect corresponding structural modifications to result.

It is not the intention to imply, however, that all character changes must be chromosomal in origin. Any influence which could effect constitutional or configurational changes in other essential constituents of the germ-cell would doubtless produce corresponding alterations in the adult. It is probable that not only changes of nuclear origin are reflected on to the cytoplasm, but that, conversely, cytoplasmic alterations may affect the nuclear constituents, for we have already seen how even the substratum may modify the enzyme factors in entire organisms such as molds and yeasts. Furthermore, there is no reason apparent why if the differences, no matter how produced, are modifications in the fundamental constitution or stereometry of the material affected, they should not persist permanently in the new germ-cells.

It would seem, in fact, that in the permanent effects of such reciprocal influences as here depicted for nucleus and cytoplasm, we might be able to account in large measure for the accumulations which have step by step been grafted on to the primitive protoplasm in its epi-

genesis toward the complex conditions of to-day, or in other words, in its racial evolution. Moreover, it is conceivable upon this basis how in later stages of phylogeny, as new chemical configurations or new chemical substances were developed, some of these could bridge back into relations with more primitively established substances and thus bring about ontogenetic short-cuts in development, or how, on the other hand, these abridgments might result in part from alterations in the more primitive molecular configurations. Racial reversions would be interpretable, at least in part, on the ground of the suppression of recently added processes or materials rather than on the reassertion of independently existing germs which had become latent.

The question arises, does not the very fact of the exactness with which the chromosomes are divided show that they are of greater fundamental importance than the cytoplasmic substances? Such a conclusion does not necessarily follow. The cytoplasmic substances of concern in development exist in the unfertilized egg apparently largely in a neutral or relatively inactive condition. The requisites are that these cytoplasmic substances be of a certain constitution and that there be a certain minimum amount of each. As insuring the presence of this indispensable minimal quantity there probably exists more or less of a surplus, but a surplus of this kind would not necessarily alter the result, as on my supposition the necessary quantitative conditions which determine the directing of the chemical reactions in the developmental processes are not brought about in this initial resting substance, but in the products of its fermentation, and the quantity of these at any given unit of time will depend upon the quantity of the ferment. Thus it is evident that by having the series of ferments accurately apportioned as we seemingly do in the chromosome, there can be an adequate quantitative and therefore qualitative regulation of the chemical processes without the controller being considered of fundamentally greater importance than the substances controlled.

I do not wish to be understood as maintaining that the nucleus or the chromosomes have no other than enzymic functions. We know that the nucleus contains highly complex proteins and it would seem improbable that all of them are concerned exclusively with matters of fermentation. There is some evidence, however, that the ferments themselves may be of the nature of nucleoproteids. If this is true it is possible that under certain conditions they operate as ferments and under other conditions as building or other necessary materials. My chief desire has been, without entering into a discussion of the manifold functions the nucleus may perform, to point out one obviously necessary function, the control of velocities in cell chemistry, that is explicable on the basis of enzymic activities, and to bring forward reasons for inferring that these have their sources in the chromosomes.

In conclusion, then, recalling the fact of the inconceivable number of stereoisomers that the proteid molecule may possess, and the fact that to make up protoplasm diverse proteins, at least, and various enzymes probably themselves of proteid nature, are required, we would seem to possess in the chemistry of relatively known chemical substances in nucleus and cytoplasm an adequate basis for interpreting the mechanism of heredity without resorting to other more hypothetical entities.

Before we embrace out of the void such new phantoms as "psychoids" or "entelechies" is it not incumbent upon us to strive still further to expand our knowledge of protein constitution and configuration? In the meantime it would seem best to look upon the organism, whether germ-cell or adult, as but the expression of an extended cycle of processes which are due to the intrinsic properties of the chemical constituents of protoplasm. Such an attitude at least has the merit of keeping within hailing distance of tangible facts and processes.

A COMPARATIVE STUDY OF THE STRUCTURE OF THE PHOTOGENIC ORGANS OF CERTAIN AMERICAN LAMPYRIDÆ

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OF the great amount of work that has been done in the production of light by living forms, not a little has been devoted to the structure of the photogenic organs. The organs whose anatomy and histology have been the subject of most of the researches have been those of the Lampyridæ. Although perhaps twenty-five species of these widely distributed insects occur within the borders of the United States proper, but little work has been done on the anatomy and histology of their luminous organs. The late Dr. Wm. H. Seaman (1) made some observations on *Photinus pyralis,* the insect which is so common in the parks in Washington in the summer, and a near relative of the *pyralis, Photinus marginellus,* has been made the subject of an extensive study by Miss Townsend, at Cornell (2). Wielowiejski (4) mentions having studied two American species, but fails to give their names. With these exceptions, however, the American Lampyridæ seem to have been neglected in the matter of histologic studies of the photogenic organs. Of the foreign Lampyridæ which have been studied, the principal species are *Lampyris noctiluca, Phausis splendidula, Phosphœnus hemipterus* and *Luciola italica,* all European species, and all belonging to different subgroups from each other and from the American insects. Many studies have also been made upon the cucuyo, *Pyrophorus noctilucus* Linn., the large tropical elaterid firefly.

It has been thought worth while, therefore, to attempt some further study of the photogenic organs of such species of Lampyridæ as are accessible here, having in view especially the determination of the similarities and differences between them and between them and other

species which had been studied previously. The two species most common here (Washington, D. C.) are *Photinus pyralis* Linn. and *Photuris pennsylvanica* Deg., and the majority of our studies have been made on them. The classification relationships between these insects and the others that have been studied may be seen from Oliver's recent catalogue (3). As already stated, *Photinus pyralis* had been studied to some extent by Seaman, and its near relative, *P. marginellus,* by Townsend, but so far as we have been able to find, no studies have been made on any species of *Photuris.*[1]

A large number of slides have been made, containing transverse, longitudinal and oblique sections of the two insects above mentioned, and a few transverse sections of *Photinus consanguineus.* With these slides comparative studies of the structure of the photogenic organs have been made. The most essential result of these studies is that in these three species the structure of the photogenic organs is practically identical, and very similar to that described for some of the other species of Lampyridæ which have been examined. Many of the drawings given by Townsend of the structures in *Photinus marginellus* may represent with equal faithfulness the corresponding structures in *Photinus pyralis* and *Photuris pennsylvanica;* our slides of *Photinus consanguineus* were not entirely satisfactory, but so far as could be seen, the structures in this insect are identical with those in its larger congener, *pyralis.*

In all three insects the luminous organ is divided into two distinct layers, the inner one being white and opaque, and serving as a reflector, and the outer being yellowish and translucent, and containing the actual photogenic mechanism. The photogenic organs, as brought out by prior studies, are penetrated from the interior of the insect outward, by innumerable tracheæ, which ramify and anastomose within the true photogenic tissue, and unite within, above the reflecting layer, to

[1] Since this was written, it has been noted that Watasé (9) made a few observations on the structures in *Photuris pennsylvanica,* but makes only a brief reference to them.

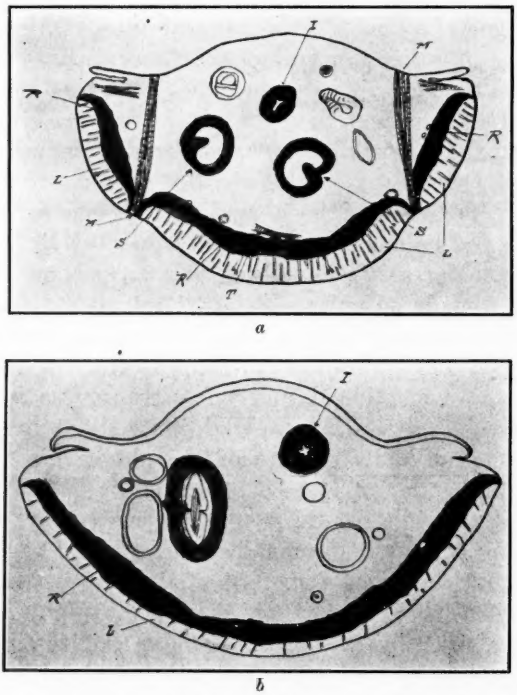

FIG. 1. Cross-sections at about the middle of the fifth abdominal segment of (*a*) *Photinus pyralis* and (*b*) *Photuris pennsylvanica*. *I*, intestine; *L*, photogenic tissue; *M*, muscle fibers; *R*, reflecting layer; *S*, spiral organs; *T*, tracheæ to photogenic organ.

form larger tracheæ; the latter lie nearly flat against the inside surface of this reflecting layer, and run diagonally outward, finally uniting almost at the spiracle with the breathing tracheæ, with which they are identical in appearance. The spiracles are on the dorsal side of the abdomen, one near either edge of each segment, and are furnished with some valvular arrangement at their orifice; the details of this structure have not yet been clearly made out. The arrangement of the smaller tracheæ and tracheoles is much the same in all three species. The tracheæ pass through the reflecting layer and the photogenic tissue perpendicularly to the surface. These tracheæ are furnished with chitinous hairs on the

interior as far as the point where they enter the reflecting layer; the presence of these hairs in tracheæ beyond this point and in the fine tracheoles, has not been observed. In their passage through the photogenic tissue, the tracheæ are surrounded by the structure referred to by Miss Townsend as the cylinder, a cylindrical mass of cells, sharply differentiated from those of the surround-

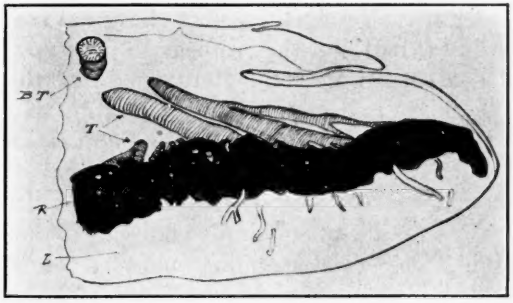

FIG. 2. Oblique section near edge of *Photinus pyralis*. *L*, photogenic tissue; *R*, reflecting layer; *T*, trachea to photogenic organ; *BT*, trachea leading to other organs. (Both of these figures are intended only as outline drawings, and no attempt has been made to show all the internal organs, or any great number of tracheæ.)

ing tissue, through which the trachea passes almost centrally. Within this cylinder the trachea throws off the numerous small branches, which at the edge of the cylinder break into the very fine tracheoles which pass into the photogenic tissue and anastomose between the cells with tracheoles from adjoining cylinders. The appearance of the large tracheæ above the luminous organ are shown in Fig. 2, drawn from an oblique section, the line of the cut being nearly parallel to the line of the larger tracheæ near the edge of the abdomen. At the lower end, just next to the superficial chitin covering the luminous segments, the main trachea subdivide into the large number of branches whose tracheoles radiate into the photogenic tissue, usually recurving slightly, so as to penetrate the tissue a short distance from the chitin.

The entire system suggests that the air is drawn in through the breathing tracheæ, and forced through the

fine passages in the true photogenic tissue, where the oxygen of the air is consumed in a biologic oxidation. In the sections of *pyralis* there are clearly seen bundles of muscle fibers on either side of the center line of the insect, which pass completely through the abdomen, almost vertically, and are attached to the exterior chitin at the top and bottom. At about the same point, other muscle fibers pass inward from the point of maximum width at each side; these fibers have not been traced to their full extent, but they appear to pass upward and toward the center near the dorsal side of the insect. These fibers are indicated in Fig. 1, *a*, at *M*. No similar muscle fibers have been observed in *Photuris*, although short lengths of muscle fiber passing vertically through the abdominal cavity have occasionally been noted, and these may be fragments of similar muscles to those in the Photinini. The corresponding muscles of *Photinus marginellus* are clearly shown in Fig. 1 of Miss Townsend's paper. Externally, the lower terminations of these bundles of muscle fibers appear as non-photogenic spots on the ventral surface of the luminous segments.

It may be well here to call attention to certain differences between *Photuris* and *Photinus*, as shown by the cross-sections of the insects. While there is a general similarity of outline in the cross-sections of the two species, the section of *Photuris* is generally a little flatter, and the ventral curvature of a somewhat larger mean radius, than in *Photinus*. Another difference has been very marked in our sections. While the thickness of the reflecting layer is about the same in both species, the layer of true photogenic tissue is much thinner, both actually and in comparison with the reflecting layer, in *Photuris* than in *Photinus;* this difference is clearly seen by reference to Fig. 1, *a* and *b*. This difference may be somewhat significant when considered in connection with the slight differences in the quality of the emitted light, and in the modes of emission of the two species. (See reference No. 8.) In *Photinus* there are two peculiar organs each consisting apparently of a thick-walled,

chitinous tube, coiled into a nearly cylindrical spiral, represented in partial section by *S, S,* in Fig. 1, *a;* these two organs appear to be glands which empty into a common duct which could be followed to the posterior extremity, and it seems possible that they are a portion of the male generative system, as they were not found in the female *pyralis,* although no spermatozoids were seen. The direction of rotation of the spiral was the reverse on the left side of the insect from that on the right. These organs were not found in the *Photuris,* although globular, glandular structures were found in approximately the same portion of the latter insect. This structure is shown in Fig. 2 of Miss Townsend's paper on *Photinus marginellus,* and in Fig. 1 of Seaman's (*Photinus pyralis*); the latter erroneously referred to it as the intestine; in our studies, the intestine of both *Photinus* and *Photuris* was seen as a nearly straight, thick-walled tube, indicated in section by *I* in *a* and *b* of Fig. 1.

The above remarks apply to the male insects. The two sexes in *Photuris* are almost indistinguishable externally; all those which we sectioned appeared to be males. In *Photinus pyralis,* however, the female differs markedly from the male. The luminous organ in the male occupies the entire ventral surface of the fifth and sixth segments of the abdomen, and the posterior portion of the fourth segment. In the female, the luminous apparatus is visible externally as a small, rectangular yellow spot, occupying about one third of the ventral area of the fifth segment of the abdomen. This organ obtains its air supply from a large trachea which extends along its forward edge, and apparently connects with the spiracles on the dorsal edges of the segment. In its finer structure, the photogenic organ of the female *pyralis* appears to be exactly like that of the male, as is to be expected.

That the photogenic process is an oxidation is scarcely to be doubted, in view of the work which has been done already. The work of one of us (McD.) with Professor

Joseph H. Kastle, of the University of Virginia, is of especial interest in this connection (6).

Our histologic methods presented no particularly new features. Most of our specimens were killed in hot 70 per cent. alcohol, stained entire in acid carmine, and mounted in paraffin. To secure proper penetration of the stain, it was found necessary to clip off the tip of the abdomen, or to slit the dorsal chitin. Osmic acid preparations were used a number of times, and in the sections of *Photinus consanguineus,* which were otherwise unsatisfactory, one per cent. osmic acid gave very good results for the fine tracheolar structure. For the study of the tissues under the dissecting microscope a good treatment was found to be to allow the detached, fresh luminous segments to soak in a mixture of equal parts of ten per cent. caustic soda and ten per cent. formaldehyde solution for three or four hours. This treatment left the tissues of both the reflecting and the active layers of the same gross appearance, though without entirely destroying the cellular structure; after being treated thus, the tracheæ and tracheoles can be seen as silvery white tubes and threads, on a background of dull, pale yellow, and may be followed down to the point of anastomosis.

It seems possible that the reflecting layer fulfils a two-fold purpose—that of reflecting the light outward, and thus increasing its intensity in the desired direction, and of protecting the insect itself from its own radiations. It has recently been shown by Coblentz (7) that the *pyralis* and other Lampyridæ contain a fluorescent material, and a number of observers have shown that fluorescent materials injected into a living animal show a higher degree of toxicity when the animal subsequently is exposed to light than if it be left in the dark.

To conclude: We have found that (*a*) the structure of the photogenic organs in *Photinus pyralis, Photinus consanguineus* and *Photuris. pennsylvanica* is practically the same, and very similar to the structures of the corresponding organs in some of the other species of Lampyridæ that have been studied; (*b*) the tracheæ from

the photogenic organs connect near the breathing spiracle with the tracheæ which supply the other organs, and that they closely resemble the latter tracheæ in structure; (*c*) the view that the photogenic process is an oxidation is borne out by the structure of the photogenic organs.

We wish to express our appreciation of the assistance of Director John F. Anderson, of the hygienic laboratory, and Dr. Norman Roberts and Mr. Geo. F. Leonard, of that laboratory, and we are indebted to Dr. E. A. Schwarz and Mr. H. S. Barber, of the U. S. National Museum, for their kindness in supplying entomologic information, and to Professor W. A. Kepner, of the University of Virginia, for criticism and advice.

No attempt will be made here to give a complete list of the references to the literature of even the histology of the luminous tissues; so far as the latter branch of the subject is concerned, it is pretty thoroughly covered by the bibliography given by Miss Townsend, and the most complete bibliography yet published of the whole subject of physiologic light is contained in Mangold's extensive and interesting review cited as reference No. 5, below.

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2. Townsend. The Histology of the Light Organs of *Photinus marginellus.* AMER. NAT., 1904, Vol. 38, pp. 127–151.
3. Olivier. Lampyridæ; Fasc. 53, Wytsman's Genera Insectorum, Brussels, 1907; Lampyridæ, Part 9, Coleopterorum Catalogus, Schenkling-Junk, Berlin, 1909.
4. Wielowiejski. Beiträge zur Kenntniss der Leuchtorgane der Insekten. *Zool. Anz.,* 1889, Vol. 12, pp. 594–600.
5. Mangold. Die Produktion von Licht. Winterstein's Handbuch der vergleichende Physiologie, Vol. III, 2d Half, pp. 225–392, Jena, 1910.
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8. McDermott. A Note on the Light-emission of some American Lampyridæ. *Canad. Entomol.,* 1910, Vol. 42, pp. 357–363.
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SHORTER ARTICLES AND DISCUSSION

A NEGLECTED PAPER ON NATURAL SELECTION IN THE ENGLISH SPARROW

In referring to Professor Bumpus's paper, "The Elimination of the Unfit as Illustrated by the Introduced Sparrow, *Passer domesticus*,"[1] as neglected, I do not intend to imply that it is unique in this respect. Several other important quantitative studies of natural selection, for instance papers by Weldon, Di Cesnola and Pearson, are in the same class. Indeed, the impression gained by reading papers commemorating the birth of Darwin and the publication of the "Origin of Species by Means of Natural Selection" is that the majority of biologists have little interest in natural selection as a scientific problem. The chief reason for this is probably the great development of experimental breeding during the last decade—a development which is a great source of satisfaction to biologists, but which has temporarily brought the study of evolution to a very one-sided stage of development.

At the time this lecture was published the statistical methods which are now considered the most suitable for dealing with such problems were not in the hands of many biologists. Recently in connection with some other work I had occasion to throw Dr. Bumpus's data[2] into statistical constants. These are published in the hope that they may suggest to some unoccupied biologist the collection of further quantitative data on the several problems presented by the introduced sparrow.

The characters dealt with are the following: (1) Total length in millimeters from tip of beak to tip of tail; (2) alar extent, the distance in millimeters from tip to tip of extended wings; (3) weight in grams; (4) length of head in millimeters from tip of beak to the occiput; (5) length of humerus in fractions of an inch; (6) length of femur in fractions of an inch; (7) length of tibio-tarsus in fractions of an inch; (8) width of skull in fractions of an inch; (9) length of sternum in fractions of an inch.

[1] Eleventh lecture before the Marine Biological Laboratory, Woods Hole, 1898; published in Biological Lectures from the Marine Biological Laboratory, 1898. Boston, Ginn and Co., 1899.

[2] Fortunately all the measurements were published.

Three classes of birds were distinguished—adult males, young males, and young and adult females.

We draw the following conclusions from the comparison of the means in Tables I–III with their probable errors.[3]

TABLE I

AVERAGES FOR ADULT MALES

Character	Survived	Perished	Difference
Total length.....	159.0571±.3154	162.0000±.3253	−2.9429±.4531
Alar extent.....	247.6857±.4333	247.3750±.4716	+ .3107±.6404
Weight (in grams)	25.4685±.1420	26.2708±.1966	− .8023±.2424
Beak and head.....	31.6143±.0709	31.6708±.0824	− .0565±.1095
Length, humerus ...	.7380±.0022	.7279±.0032	+ .0101±.0038
Length of femur.....	.7168±.0025	.7061±.0027	+ .0107±.0037
Tibio-tarsus.	1.1353±.0041	1.1202±.0051	+ .0151±.0065
Width of skull.....	.6025±.0016	.6033±.0017	− .0008±.0023
Keel of sternum.....	.8576±.0042	.8458±.0045	+ .0118±.0062

TABLE II

AVERAGES FOR YOUNG MALES

Character	Survived	Perished	Difference
Total length.....	159.6875±.4978	162.2499± .7291	−2.5624± .8828
Alar extent.....	246.8125±.7936	247.9167±1.2976	−1.1042±1.5213
Weight (in grams).	25.4938±.2040	26.2667± .3208	− .7729± .3801
Beak and head.....	31.8688±.1190	31.3249± .1138	+ .5439± .1646
Length, humerus....	.7416±.0039	.7347± .0055	+ .0069± .0067
Length of femur.....	.7162±.0046	.7153± .0050	+ .0009± .0068
Tibio-tarsus	1.1367±.0091	1.1393± .0071	− .0026± .0115
Width of skull.....	.6078±.0024	.5993± .0035	+ .0085± .0042
Keel of sternum	.8514±.0060	.8427± .0064	+ .0087± .0088

TABLE III

AVERAGES FOR ALL FEMALES

Character	Survived	Perished	Difference
Total length.....	157.3810±.4774	158.4286±.4859	−1.0476±.6811
Alar extent.....	241.0000±.6009	241.5714±.7142	− .5714±.9333
Weight (in grams)..	24.6190±.153	25.3357±.2054	− .7167±.2561
Beak and head.....	31.4333±.1047	31.4786±.1068	− .0453±.1495
Length, humerus....	.7283±.0024	.7260±.0032	+ .0023±.0040
Length of femur.....	.7148±.0029	.7098±.0036	+ .0050±.0046
Tibio-tarsus.....	1.1436±.0042	1.1310±.0043	+ .0126±.0060
Width of skull.....	.6001±.0019	.6016±.0031	− .0015±.0036
Keel of sternum.....	.8193±.0043	.8207±.0037	− .0014±.0057

[3] For the individual comparisons those differences less than the probable error will be considered of no significance, those between one and two times their probable errors as possibly significant, and those over thrice their probable errors as probably significant.

TABLE IV

STANDARD DEVIATIONS FOR ADULT MALES

Character	Survived	Perished	Difference
Total length	2.7666±.2230	2.3629±.2300	+.4037±.3203
Alar extent	3.8005±.3064	3.4255±.3335	+.3750±.4529
Weight (in grams)	1.2451±.1004	1.4276±.1390	−.1825±.1715
Beak and head	.6220±.0501	.5982±.0582	+.0238±.0768
Length, humerus	.0196±.0016	.0230±.0022	−.0034±.0027
Length of femur	.0222±.0018	.0199±.0019	+.00 3±.0026
Tibio-tarsus	.0355±.0029	.0370±.0036	−.0015±.0046
Width of skull	.0317±.0011	.0123±.0012	+.0194±.0016
Keel of sternum	.0366±.0030	.0325±.0032	+.0041±.0044

TABLE V

STANDARD DEVIATIONS FOR YOUNG MALES

Character	Survived	Perished	Difference
Total length	2.9521±.3520	3.7444±.5155	− .7923± .6242
Alar extent	4.7066±.5612	6.6641±.9175	−1.9575±1.0755
Weight (in grams)	1.2101±.1443	1.6474±.2268	− .4373± .2687
Beak and head	.7060±.0842	.5847±.0805	+ .1213± .1166
Length, humerus	.0234±.0028	.0282±.0039	− .0048± .0048
Length of femur	.0272±.0032	.0258±.0035	+ .0014± .0047
Tibio-tarsus	.0537±.0064	.0365±.0050	+ .0172± .0081
Width of skull	.0141±.0017	.0180±.0025	− .0039± .0030
Keel of sternum	.0356±.0042	.0331±.0046	+ .0025± .0062

TABLE VI

STANDARD DEVIATIONS FOR ALL FEMALES

Character	Survived	Perished	Difference
Total length	3.2437±.3376	3.8119±.3436	− .5682±.4817
Alar extent	4.0825±.4249	5.6025±.5050	−1.5200±.6600
Weight (in grams)	1.0400±.1082	1.6112±.1452	− .5712±.1811
Beak and head	.7114±.0740	.8381±.0755	− .1267±.1054
Length, humerus	.0160±.0017	.0255±.0023	− .0095±.0029
Length of femur	.0197±.0021	.0279±.0025	− .0082±.0033
Tibio-tarsus	.0287±.0030	.0336±.0030	− .0049±.0042
Width of skull	.0128±.0013	.0245±.0022	− .0117±.0026
Keel of sternum	.0292±.0030	.0286±.0026	+ .0006±.0040

In all three series the individuals which survive are shorter than those which perish. The probable errors support in a very satisfactory manner the conclusion, "that when nature selects, through the agency of winter storms of this particular kind of severity, those sparrows which are short stand a better chance of surviving." For weight the results for the three series are also consistent in sign, and even when taken individually indicate

with a considerable degree of probability that the heavier birds are the least able to withstand the vicissitudes of the February sleet and snow. In all three series the length of the humerus is longer in the birds which survive, and in the group of adult males the difference is perhaps statistically significant. The same is true for the length of the femur, but the results are again insignificant except in the adult males where they are perhaps statistically trustworthy. In the adult males and in the adult and young females the length of the tibio-tarsus seems to be longer in the survivors, but the result is insignificant for the young males.

If selective elimination be a reality in nature one would not expect all of the characters of a series of individuals which perished when exposed to a given set of unfavorable conditions to differ from the same characters in the individuals which survive, and this for the simple reason that variations in many characters may not be of vital importance to the individual—in short, not of selective value.

The constants seem to me to justify no conclusion concerning the length of the sternum. For alar extent all three differences individually considered are insignificant; taken comparatively two are negative and one positive in sign. Apparently variations in the spread of wing have under the particular conditions[4] no significance in determining the chances of survival. The young males which survived have longer skulls (tip of beak to the occiput) than those which perished, and the difference seems to be significant in comparison with its probable error, but in the other two classes of birds the differences are not merely statistically insignificant but negative in sign.

Tables IV–VI show the standard deviations and their probable error. These are essential in calculating the probable errors of the means and in testing the hypothesis of a reduction in variability by selective elimination. Bumpus has discussed this question in detail in his lecture, but to me it seems that the standard deviations as given here do not justify any final conclusions concerning the relation of selection to variability: the problem is too complicated and the data are too few. As in other evolutionary problems we need more measurements. When these are available

[4] "Were the eliminative agent, for example, a severe northerly wind of protracted duration, the alar extent might then enter in as a factor of considerable selective value."

not only type and variability but correlation[5] will be open for investigation.

Looking at the tables of constants, the cautious biometrician will hesitate to say that Professor Bumpus has *proved* his point. The data available are too scanty to justify dogmatic assertions. But the work is so suggestive and the results so convincing that it is difficult to understand why zoologists have not followed it up by other studies of a comparable nature. To be sure, opportunities of this particular kind do not occur every winter, but there are other sources of elimination active in nature, and one of the most important tasks before those interested in the problems which Darwin pointed out to biologists, is to determine whether the individuals which survive are able to do so because of certain structural peculiarities, while those which perish are eliminated because they are in the degree of development or in the correlation of their parts structurally unfit.

J. ARTHUR HARRIS.

[5] Compare besides Bumpus's suggestion on this point, the arguments of Brooks in his "Foundations of Zoology," Lectures VI–VIII, and the hypothesis of Crampton, in *Journ. Exp. Zool.*, 2: 425–430, 1905.

NOTES AND LITERATURE

BIOMETRICS

An Introduction to Statistical Methods

In spite of the great development of biometric work, and of the application of statistical conceptions and methods in a number of fields of science other than biological, during the last decade there has been produced up to the present time no fully satisfactory introduction to the elementary principles of modern statistical methods. The books which have appeared in this field have been, broadly speaking, either (*a*) too technical and advanced in their treatment, or (*b*) compilations of formulæ with so little in the way of guiding principles as actually to lead any but the already expert into many difficulties, or (*c*) incomplete, incorrect and superficial at vital points, or finally, (*d*) have appealed to a very limited class of readers by developing the subject in direct relation to a narrow field of science only. This need for a comprehensive, elementary and sound introduction to statistical methods is admirably met in a recently published book by Yule.[1]

The subject is treated under three main heads as follows: (I) The Theory of Attributes, (II) The Theory of Variables, (III) The Theory of Sampling. In the first part the author deals with the logical basis of statistical theory, a field which is essential to a proper understanding of the subject, and in which he is, by the extent and character of his original investigations, qualified to speak with unique authority. Successive chapters in this portion of the work deal with Notation and Terminology, Consistence, Association, Partial Association, Manifold Classification.

The second part of the book takes up the discussion of frequency distributions and their physical constants, and the elementary theory of correlation and its applications, ending with an account of multiple and partial correlation. Here we are dealing with matters of immediate practical importance in the application of statistical methods to all kinds of scientific problems. It would be difficult to say too much in commendation of the author's method of treating these subjects. No knowledge

[1] Yule, G. Udny, "An Introduction to the Theory of Statistics," London (Chas. Griffin & Co.), 1911, pp. xiii + 376.

of mathematics beyond algebra up to the binomial theorem is presumed, yet the subject is developed in such a simple, lucid and at the same time thorough way as to give the reader a real and adequate grasp not only of the technique of the methods, but also of their origin and significance. Numerical examples drawn from a wide range of materials are given at every stage and worked out in detail. Particular attention is paid to guiding the unwary beginner around the numerous pitfalls which beset the statistical pathway. Chapters are devoted to the methods of arranging data in the form of frequency distributions, determining centering constants (arithmetic, geometric and harmonic means, mode, median, etc.), variation or "dispersion" measuring constants, and coefficients of correlation. The treatment of correlation is particularly comprehensive and practical.

The last section of the book deals with the general subject of "probable errors." The theory of fluctuations in statistical measures due to random sampling is developed first in relation to the theory of attributes and then in relation to the more complex theory of variables. The discussion of the simple sampling of attributes leads up in a straightforward way through the point binomial to the normal curve of errors, and the normal correlation surface.

Each chapter throughout the book is followed by a short list of selected titles of original papers, and a series of practical problems to be worked out by the student. Appendices give short bibliographies of calculating tables, tables of functions, etc., and general works on the mathematical theory of statistics and the theory of probability. A list of answers and hints in regard to the problems and a full index complete the volume.

Altogether the book is a notable one. Those who are familiar with Yule's paper "On the Theory of Correlation" (published in the *Journal of the Royal Statistical Society* in 1897) which has become one of the classics of biometric literature will be prepared to welcome the present work. It is marked throughout by the same clearness, directness and appreciation of the difficulties of the beginner which distinguished that memoir. For the non-mathematical student desirous of obtaining a sound working knowledge of the elements of modern statistical theory this book will be of the greatest value. In the field which it covers it is without a peer.

RAYMOND PEARL.